MECHANISMS OF BIODIVERSITY–PRODUCTIVITY RELATIONSHIPS

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“Yet political will to address the biodiversity crisis will only result from an increased public understanding of biodiversity and its relation to human well-being.”

(Secretariat of the Convention on Biological Diversity 2006,
Global biodiversity outlook 2. Montreal, p. 54)

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General Introduction

Background

The diversity of life on Earth is changing more rapidly than at any time in human history. These changes include the reduction of population sizes within a disconcerting number of plant and animal species and the shrinkage of their distribution areas. Other species spread to areas they had never inhabited where some of them cause serious damage to the native flora or fauna. Human activities are largely responsible for these changes in biodiversity which are leading to a calamitous loss of species diversity worldwide (Millennium Ecosystem Assessment 2005; Secretariat of the Convention on Biological Diversity 2006).

The local and global extinction of species impairs the integrity of ecosystems with potential consequences for humans' sustenance, health, well-being and enjoyment of life (Chapin *et al.* 2000; Díaz *et al.* 2006). Understanding the role of biodiversity for ecosystem functioning is therefore of prime interest and has become an important topic in ecological research. However, exploring the relationship between biodiversity and ecosystem functioning in natural ecosystems is challenging because abiotic conditions and biological interactions may have intermingled effects on an ecosystem property or function. Further complication arises from the fact that the number of species within an ecosystem may be the cause as well as the effect of an ecosystem function, in particular of aboveground primary productivity (Schmid 2002; Gross & Cardinale 2007). Experiments with manipulated biodiversity levels are therefore an indispensable tool for clarifying the role of biodiversity for ecosystem functioning (Schmid *et al.* 2002).

During the past two decades, numerous of such experiments have provided valuable insights into biodiversity–ecosystem functioning relationships in various ecosystems, ranging from bacterial communities in microcosms (e.g. Bell *et al.* 2005) to tree plantations on multiple hectare field sites (e.g. Potvin & Gotelli 2008). Most experimental field trials have been conducted in grasslands and aimed at quantifying biodiversity effects on biomass production (Balvanera *et al.* 2006). This bias may be explained by the feasibility of setting up such experiments (taking advantage of herbaceous plants being sessile and fast growing), the high abundance of grassland ecosystems world-wide and the dependency of nearly all life on Earth on the capacity of plants to produce organic compounds through photosynthesis, i.e. on primary productivity.

The majority of these experiments indicate a positive relationship between biodiversity ecosystem functioning (Balvanera *et al.* 2006; Cardinale *et al.* 2006). However, we still know relatively little about the mechanisms that explain why increasing species richness in grasslands usually increases primary productivity (e.g. Tilman *et al.* 1996; Hector *et al.* 1999;

Tilman *et al.* 2001; Van Ruijven & Berendse 2003; Hooper & Dukes 2004; Roscher *et al.* 2005; Van Ruijven & Berendse 2005; Isbell *et al.* 2008; Marquard *et al.* 2009b; Van Ruijven & Berendse 2009), invasion resistance (Knops *et al.* 1999; Levine 2000; Fargione & Tilman 2005a; Fargione & Tilman 2005b; Mwangi *et al.* 2007) and temporal stability of plant community biomass (Tilman *et al.* 2006; Van Ruijven & Berendse 2007; Isbell *et al.* 2009).

Mechanistic explanations of how the number of species (or any other component of biodiversity, such as genotypes or functional groups of species) may enhance ecosystem functioning centre on the following two ideas. Positive effects may either result from different species acting together or from a single species with favourable characteristics dominating the community. More precisely, if different species use limited resources more efficiently than conspecific individuals, ecosystem functioning should increase with diversity due to the concerted effect of multiple species (known as complementarity, Tilman *et al.* 1997a; Loreau 1998). The same is true if direct positive interactions between different species are beneficial for their performance (known as facilitation, Callaway 1997; Callaway & Walker 1997). On the other hand, a mixture of species may be dominated by a species that performs particularly well with regard to the ecosystem function in question (known as selection, Loreau & Hector 2001). If communities are composed from a limited pool of species, the chance of better competitors being present increases with diversity (known as sampling, Aarssen 1997; Wardle 1999). Because better competitors produce more biomass than the remaining species community productivity should increase with increasing species richness, in this case due to the effect of a single species (Tilman *et al.* 1997b). In other words, the sampling effect mechanism implicitly assumes that the species most productive in monoculture dominate in mixture. In the strict sense, the 'selection effect' according to Loreau & Hector (2001) measures the covariance between a species performance in monoculture and in mixture and 'sampling' denotes the higher probability to choose a particular species from a species pool at higher diversity (Hooper *et al.* 2005). The selection effect includes the special case of the sampling effect, and is also able to consider other scenarios where unproductive species dominate in mixture. However, in the literature the terms 'selection' and 'sampling' are sometimes used interchangeably (e.g. Huston 1997; Wardle 1999; Bell *et al.* 2005; Cardinale *et al.* 2006).

Regarding biodiversity–productivity relationships in grasslands, a large body of literature is now available that reports on experiments aiming at disentangling effects of multiple species acting together (complementarity effects and facilitation) from selection effects and sampling (e.g. Lepš *et al.* 2001; Špaèková & Lepš 2001; Tilman *et al.* 2001;

Hector *et al.* 2002; Polley *et al.* 2003; Fargione & Tilman 2005b; Roscher *et al.* 2005; Fargione *et al.* 2007; Roscher *et al.* 2007; Isbell *et al.* 2008; Wacker *et al.* 2008; Marquard *et al.* 2009b) or on meta-analyses with the same intent (Cardinale *et al.* 2006; Cardinale *et al.* 2007). Another recurring question has been whether positive effects of species richness on biomass production are largely explained by the presence of legumes that improve the availability of nitrogen for other species (Huston & McBride 2002; Mulder *et al.* 2002; Spehn *et al.* 2002; Hector *et al.* 2007; Temperton *et al.* 2007). There is now considerable evidence that other beneficial interactions than between legumes and non-legumes contribute to increased productivity in species-rich communities (Van Ruijven & Berendse 2003; Hector *et al.* 2007; Marquard *et al.* 2009b; Van Ruijven & Berendse 2009). However, distinguishing effects caused by the traits of particular species from effects caused by species interactions has remained important for the identification of the general mechanisms by which diversity increases productivity.

Beyond that, research focuses increasingly on exploring particular processes in more detail, e.g. the complementary use of water (Verheyen *et al.* 2008), nitrogen (Fornara & Tilman 2009; von Felten *et al.* 2009) or aboveground space (Lorentzen *et al.* 2008; Wacker 2008). Furthermore, the consideration of size–density relationships (Roscher *et al.* 2007; Marquard *et al.* 2009a), the role of pathogens (Mitchell *et al.* 2003; De Deyn *et al.* 2004; Bell *et al.* 2006; Petermann *et al.* 2008) as well as phylogeny (Cadotte *et al.* 2008; King 2009) holds great promise for achieving a mechanistic understanding of biodiversity–productivity relationships.

Thesis outline

In this thesis, I explore mechanisms of biodiversity–productivity relationships in grasslands. For my analyses, I use aboveground biomass data (as a surrogate for primary productivity) from the Jena Experiment, a large-scale biodiversity experiment in Germany that addresses the role of plant diversity for element cycling and trophic interactions (Roscher *et al.* 2004). Details on the design are given in the individual chapters of this thesis.

In **chapter 1**, I explore the role of different biodiversity components (number of species, number of functional groups of species, presence of particular functional groups and their proportional abundance) for community biomass production. I assess the contributions of complementarity and selection effects to the enhanced performance of species-rich communities and make full use of the sophisticated design of the Jena Experiment. Its outstanding characteristics are large plots sizes (20 x 20 m), a species pool containing 60

species, the presence of all these species in two replicate monocultures, the near-orthogonal combination of the species richness and functional group richness treatments and the wide range of sown proportions of a particular functional group per species richness level. I identify species richness as well as functional group composition as important drivers of a positive biodiversity–productivity relationship and present strong evidence for transgressive overyielding among functional groups.

In **chapter 2**, I examine temporal fluctuations in net biodiversity effects, i.e. in the differences between yields of mixtures and expected values derived from the yield of the composing species in monoculture. I analyze whether changes in mean net effects over time resulted predominantly from an increase of species performance in mixture or from a degradation of monocultures. I show that monocultures and mixtures differed with regard to temporal trends in biomass production, possibly due to negative plant–soil feedbacks or an inverse relationship between the severity of foliar pathogen attacks and plant species richness. However, I show that the increase in the net effect that occurred from 2005–2007 in the Jena Experiment was not predominantly caused by a decreasing performance of species in monoculture but by an enhanced performance of species in mixture.

Chapter 3 is the documentation of plant-related data from the Jena Experiment. The data set contains species-specific biomass and cover data as well as community leaf area index (LAI) and mean vegetation height. Most but not all variables were measured twice during the years 2002–2008. This data set will be made publicly available for new studies on a variety of questions about how plant community composition and structure responds to changes in species richness and functional diversity over time.

In **chapter 4**, I explore whether positive biodiversity effects on aboveground productivity resulted from an increase in the number or the size of individual plants. The relationship between plant size and density within a population may strongly affect mortality and reproduction and may therefore have further consequences for the genetic diversity within the population as well as for community composition. I show that diversity-induced changes in productivity were mainly caused by diversity-induced changes in plant density. Interestingly, diversity-independent increases in productivity were related to an increase in plant size.

Chapter references

Aarssen L. W. (1997). High productivity in grassland ecosystems: effected by species diversity or productive species? *Oikos*, **80**, 183-184.

Balvanera P., Pfisterer A. B., Buchmann N., He J.-S., Nakashizuka T., Raffaelli D. & Schmid B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, **9**, 1-11.

Bell T., Newman J. A., Silverman B. W., Turner S. L. & Lilley A. K. (2005). The contribution of species richness and composition to bacterial services. *Nature*, **436**, 1157-1160.

Bell T., Freckleton R. P. & Lewis O. T. (2006). Plant pathogens drive density-dependent seedling mortality in a tropical tree. *Ecology Letters*, **9**, 569-574.

Cadotte M. W., Cardinale B. J. & Oakley T. H. (2008). Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 17012-17017.

Callaway R. M. (1997). Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia*, **112**, 143-149.

Callaway R. M. & Walker L. R. (1997). Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, **78**, 1958-1965.

Cardinale B. J., Srivastava D. S., Duffy J. E., Wright J. P., Downing A. L., Sankaran M. & Jouseau C. (2006). Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, **443**, 989-992.

Cardinale B. J., Wrigh J. P., Cadotte M. W., Carroll I. T., Hector A., Srivastava D. S., Loreau M. & Weis J. J. (2007). Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences*, **104**, 18123-18128.

Chapin F. S., Zavaleta E. S., Eviner V. T., Naylor R. L., Vitousek P. M., Reynolds H. L., Hooper D. U., Lavorel S., Sala O. E., Hobbie S. E., Mack M. C. & Díaz S. (2000). Consequences of changing biodiversity. *Nature*, **405**, 234-242.

De Deyn G. B., Raaijmakers C. E., Van Ruijven J., Berendse F. & Van der Putten W. H. (2004). Plant species identity and diversity effects on different trophic levels of nematodes in the soil food web. *Oikos*, **106**, 576-586.

Díaz S., Fargione J., Chapin F. S. & Tilman D. (2006). Biodiversity loss threatens human well-being. *Plos Biology*, **4**, 1300-1305.

Fargione J. & Tilman D. (2005a). Niche differences in phenology and rooting depth promote coexistence with a dominant C-4 bunchgrass. *Oecologia*, **143**, 598-606.

Fargione J., Tilman D., Dybzinski R., Hille Ris Lambers J., Clark C., Harpole W. S., Knops J. M. H., Reich P. B. & Loreau M. (2007). From selection to complementarity: shifts in the causes of biodiversity-productivity relationships in a long-term biodiversity experiment. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **274**, 871-876.

Fargione J. E. & Tilman D. (2005b). Diversity decreases invasion via both sampling and complementarity effects. *Ecology Letters*, **8**, 604-611.

Fornara D. A. & Tilman D. (2009). Ecological mechanisms associated with the positive diversity-productivity relationship in an N-limited grassland. *Ecology*, **90**, 408-418.

Gross K. & Cardinale B. J. (2007). Does species richness drive community production or vice versa? Reconciling historical and contemporary paradigms in competitive communities. *The American Naturalist*, **170**, 207-220.

Hector A., Schmid B., Beierkuhnlein C., Caldeira M. C., Diemer M., Dimitrakopoulos P. G., Finn J. A., Freitas H., Giller P. S., Good J., Harris R., Högberg P., Huss-Danell K., Joshi J., Jumpponen A., Körner C., Leadley P. W., Loreau M., Minns A., Mulder C. P. H., O'Donovan G., Otway S. J., Pereira J. S., Prinz A., Read D. J., Scherer-Lorenzen M., Schulze E.-D., Siamantziouras A.-S. D., Spehn E. M., Terry A. C., Troumbis A. Y., Woodward F. I., Yachi S. & Lawton J. H. (1999). Plant diversity and productivity experiments in European grasslands. *Science*, **286**, 1123-1127.

Hector A., Bazeley-White E., Loreau M., Otway S. & Schmid B. (2002). Overyielding in grassland communities: testing the sampling effect hypothesis with replicated biodiversity experiments. *Ecology Letters*, **5**, 502-511.

Hector A., Joshi J., Scherer-Lorenzen M., Schmid B., Spehn E. M., Wacker L., Weilenmann M., Bazeley-White E., Beierkuhnlein C., Caldeira M. C., Dimitrakopoulos P. G., Finn J. A., Huss-Danell K., Jumpponen A., Leadley P. W., Loreau M., Mulder C. P. H., Neßhöver C., Palmborg C., Read D. J., Siamantziouras A. S. D., Terry A. C. & Troumbis A. Y. (2007). Biodiversity and ecosystem functioning: reconciling the results of experimental and observational studies. *Functional Ecology*, **21**, 998-1002.

Hooper D. U. & Dukes J. S. (2004). Overyielding among plant functional groups in a long-term experiment. *Ecology Letters*, **7**, 95-105.

Hooper D. U., Chapin F. S., Ewel J. J., Hector A., Inchausti P., Lavorel S., Lawton J. H., Lodge D. M., Loreau M., Naeem S., Schmid B., Setälä H., Symstad A. J., Vandermeer J. & Wardle D. A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3-35.

Huston M. A. (1997). Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, **110**, 449-460.

Huston M. A. & McBride A. C. (2002). Evaluating the relative strengths of biotic versus abiotic controls on ecosystem processes. In: *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives* (eds. Loreau M., Naeem S. & Inchausti P.). Oxford University Press Oxford, pp. 47-60.

Isbell F. I., Losure D. A., Yurkonis K. A. & Wilsey B. J. (2008). Diversity-productivity relationships in two ecologically realistic rarity-extinction scenarios. *Oikos*, **117**, 996-1005.

Isbell F. I., Polley H. W. & Wilsey B. J. (2009). Biodiversity, productivity and the temporal stability of productivity: patterns and processes. *Ecology Letters*, **12**, 443-451.

King I. (2009). The need for the incorporation of phylogeny in the measurement of biological diversity, with special reference to ecosystem functioning research. *Bioessays*, **31**, 107-116.

Knops J. M. H., Tilman D., Haddad N. M., Naeem S., Mitchell C. E., Haarstad J., Ritchie M. E., Howe K. M., Reich P. B., Siemann E. & Groth J. (1999). Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters*, **2**, 286-293.

Lepš J., Brown V. K., Len T. A. D., Gormsen D., Hedlund K., Kailova J., Korthals G. W., Mortimer S. R., Rodriguez-Barrueco C., Roy J., Regina I. S., Van Dijk C. & Van der Putten W. H. (2001). Separating the chance effect from other diversity effects in the functioning of plant communities. *Oikos*, **92**, 123-134.

Levine J. M. (2000). Species diversity and biological invasions: relating local process to community pattern. *Science*, **288**, 852-854.

Loreau M. (1998). Biodiversity and ecosystem functioning: a mechanistic model. *Proceedings of the National Academy of Sciences*, **95**, 5632-5636.

Loreau M. & Hector A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, **412**, 72-76.

Lorentzen S., Roscher C., Schumacher J., Schulze E.-D. & Schmid B. (2008). Species richness and identity affect the use of aboveground space in experimental grasslands. *Perspectives in Plant Ecology Evolution and Systematics*, **10**, 73-87.

Marquard E., Weigelt A., Roscher C., Gubsch M., Lipowsky A. & Schmid B. (2009a). Positive biodiversity-productivity relationship due to increased plant density. *Journal of Ecology*, **doi: 10.1111/j.1365-2745.2009.01521.x**.

Marquard E., Weigelt A., Temperton V. M., Roscher C., Schumacher J., Buchmann N., Fischer M., Weisser W. W. & Schmid B. (2009b). Plant species richness and functional composition drive overyielding in a 6-year grassland experiment. *Ecology*, **in press**.

Millennium Ecosystem Assessment (2005). In: *Ecosystems and human well-being: biodiversity synthesis*. World Resources Institute Washington, DC.

Mitchell C. E., Reich P. B., Tilman D. & Groth J. V. (2003). Effects of elevated CO2, nitrogen deposition, and decreased species diversity on foliar fungal plant disease. *Global Change Biology*, **9**, 438-451.

Mulder C. P. H., Jumpponen A., Högberg P. & Huss-Danell K. (2002). How plant diversity and legumes affect nitrogen dynamics in experimental grassland communities. *Oecologia*, **133**, 412-421.

Mwangi P. N., Schmitz M., Scherber C., Roscher C., Schumacher J., Scherer-Lorenzen M., Weisser W. W. & Schmid B. (2007). Niche pre-emption increases with species richness in experimental plant communities. *Journal of Ecology*, **95**, 65-78.

Petermann J. S., Fergus A. J. F., Turnbull L. A. & Schmid B. (2008). Janzen-Connell effects are widespread and strong enough to maintain diversity in grasslands. *Ecology*, **89**, 2399-2406.

Polley H. W., Wilsey B. J. & Derner J. D. (2003). Do species evenness and plant density influence the magnitude of selection and complementarity effects in annual plant species mixtures? *Ecology Letters*, **6**, 248-256.

Potvin C. & Gotelli N. J. (2008). Biodiversity enhances individual performance but does not affect survivorship in tropical trees. *Ecology Letters*, **11**, 217-223.

Roscher C., Schumacher J., Baade J., Wilcke W., Gleixner G., Weisser W. W., Schmid B. & Schulze E.-D. (2004). The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. *Basic and Applied Ecology*, **5**, 107-121.

Roscher C., Temperton V. M., Scherer-Lorenzen M., Schmitz M., Schumacher J., Schmid B., Buchmann N., Weisser W. W. & Schulze E.-D. (2005). Overyielding in experimental grassland communities - irrespective of species pool or spatial scale. *Ecology Letters*, **8**, 419-429.

Roscher C., Schumacher J., Weisser W. W., Schmid B. & Schulze E. D. (2007). Detecting the role of individual species for overyielding in experimental grassland communities composed of potentially dominant species. *Oecologia*, **154**, 535-549.

Schmid B. (2002). The species richness-productivity controversy. *Trends in Ecology and Evolution*, **17**, 113-114.

Schmid B., Hector A., Huston M., Inchausti P., Nijs I., Leadley P. & Tilman D. (2002). The design and analysis of biodiversity experiments. In: *Biodiversity and ecosystem functioning: Synthesis and Perspectives* (eds. Loreau M., Naeem S. & Inchausti P.). Oxford University Press New York, pp. 61-75.

Secretariat of the Convention on Biological Diversity (2006). Global biodiversity outlook 2. Montreal, p. 81 + vii pages.

Špaèková I. & Lepš J. (2001). Procedure for separating the selection effect from other effects in diversity-productivity relationship. *Ecology Letters*, **4**, 585-594.

Spehn E. M., Scherer-Lorenzen M., Schmid B., Hector A., Caldeira M. C., Dimitrakopoulos P. G., Finn J. A., Jumpponen A., O'Donnovan G., Pereira J. S., Schulze E. D., Troumbis A. Y. & Körner C. (2002). The role of legumes as a component of biodiversity in a cross-European study of grassland biomass nitrogen. *Oikos*, **98**, 205-218.

Temperton V. M., Mwangi P. N., Scherer-Lorenzen M., Schmid B. & Buchmann N. (2007). Positive interactions between nitrogen-fixing legumes and four different neighbouring species in a biodiversity experiment. *Oecologia*, **151**, 190-205.

Tilman D., Wedin D. & Knops J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, **379**, 718-720.

Tilman D., Lehman C. L. & Thomson K. T. (1997a). Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences*, **94**, 1857-1861.

Tilman D., Lehman C. L. & Thomson K. T. (1997b). Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences*, **94**, 1857-1861.

Tilman D., Reich P. B., Knops J., Wedin D., Mielke T. & Lehman C. (2001). Diversity and productivity in a long-term grassland experiment. *Science*, **294**, 843-845.

Tilman D., Reich P. B. & Knops J. M. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, **441**, 629-632.

Van Ruijven J. & Berendse F. (2003). Positive effects of plant species diversity on productivity in the absence of legumes. *Ecology Letters*, **6**, 170-175.

Van Ruijven J. & Berendse F. (2005). Diversity-productivity relationships: initial effects, long-term patterns, and underlying mechanisms. *Proceedings of the National Academy of Sciences*, **102**, 695-700.

Van Ruijven J. & Berendse F. (2007). Contrasting effects of diversity on the temporal stability of plant populations. *Oikos*, **116**, 1323-1330.

Van Ruijven J. & Berendse F. (2009). Long-term persistence of a positive plant diversity–productivity relationship in the absence of legumes. *Oikos*, **118**, 101-106.

Verheyen K., Bulteel H., Palmborg C., Olivie B., Nijs I., Raes D. & Muys B. (2008). Can complementarity in water use help to explain diversity-productivity relationships in experimental grassland plots? *Oecologia*, **156**, 351-361.

von Felten S., Hector A., Buchmann N., Niklaus P., A., Schmid B. & Scherer-Lorenzen M. (2009). Belowground nitrogen partitioning in experimental grassland plant communities of varying species richness. *Ecology*, **90**, 1389-1399.

Wacker L. (2008). Diversity effects in early- and mid-successional experimental grasslands. PhD-Thesis. Mathematisch-naturwissenschaftliche Fakultät, University of Zürich, Zürich.

Wacker L., Baudois O., Eichenberger-Glinz S. & Schmid B. (2008). Environmental heterogeneity increases complementarity in experimental grassland communities. *Basic and Applied Ecology*, **9**, 467-474.

Wardle D. A. (1999). Is "sampling effect" a problem for experiments investigating biodiversity-ecosystem function relationships? *Oikos*, **87**, 403-407.

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Chapter 1

Plant species richness and functional composition drive overyielding in a 6-year grassland experiment

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Abstract

Plant diversity has been shown to increase community biomass in experimental communities but the mechanisms resulting in such positive biodiversity effects have remained largely unknown. We used a large-scale 6-year biodiversity experiment to examine how aboveground community biomass in grasslands is affected by different components of plant diversity and thereby infer the mechanisms that may underlie positive biodiversity effects. As components of diversity we defined the number of species (1–16), number of functional groups (1–4), presence of functional groups (legumes, tall herbs, small herbs and grasses) and proportional abundance of functional groups. Using linear models, replacement series on the level of functional groups and additive partitioning on the level of species we explored whether the observed biodiversity effects originated from disproportionate effects of single functional groups or species or from positive interactions between them.

Aboveground community biomass was positively related to the number of species measured across functional groups as well as to the number of functional groups measured across different levels of species richness. Furthermore, increasing the number of species within functional groups increased aboveground community biomass, indicating that species within functional groups were not redundant with respect to biomass production. A positive relationship between the number of functional groups and aboveground community biomass within a particular level of species richness suggested that complementarity was larger between species belonging to different rather than to the same functional groups. The presence of legumes or tall herbs had a strong positive impact on aboveground community biomass whereas the presence of small herbs or grasses had on average no significant effect. Two- and 3-way interactions between functional group presences were weak, suggesting that their main effects were largely additive. Replacement series analyses on the level of functional groups revealed strong transgressive overyielding and relative yields > 1 indicating facilitation. On the species level, we found strong complementarity effects which increased over time while selection effects due to disproportionate contributions of particular species decreased over time. We conclude that transgressive overyielding between functional groups and species richness effects within functional groups caused the positive biodiversity effects on aboveground community biomass in our experiment.

Keywords

Biodiversity, complementarity, ecosystem functioning, functional groups, Jena Experiment, replacement series, transgressive overyielding

Introduction

Global biodiversity is declining at a fast rate (Thomas *et al.* 2004; Van Vuuren *et al.* 2006) and the predicted loss of species in the near future has the potential to impair ecosystem functioning (Chapin *et al.* 2000; Hooper *et al.* 2005). Experiments with manipulated diversity levels have demonstrated repeatedly that ecosystem processes are indeed positively affected by the number of and differences among species in a community (reviewed in Balvanera *et al.* 2006; Cardinale *et al.* 2006; Díaz *et al.* 2006). Two non-exclusive mechanisms are assumed to be the main drivers of such positive biodiversity effects (Aarssen 1997; Huston 1997; Tilman *et al.* 1997b; Loreau 1998): (1) a higher resource-use efficiency or positive interactions within diverse mixtures (referred to as complementarity or facilitation) and (2) the presence of particular species or functional groups (FGs) in diverse mixtures that have a disproportionate effect on a property at the community level (referred to as sampling, selection or dominance).

We used a large-scale 6-year biodiversity experiment (Jena Experiment) to examine the effect of plant diversity on aboveground community biomass in grasslands and the relative contributions of complementarity (including facilitation) and selection effects (including sampling and dominance) to positive biodiversity effects.

Complementarity is assumed to be larger between species belonging to different FGs than between species belonging to the same FG (Díaz & Cabido 2001; Hooper *et al.* 2002). Therefore, if complementarity was the major mechanism underlying positive biodiversity effects, FG richness (number of FGs) and species richness (number of species) across FGs should more strongly affect ecosystem functioning than species richness within FGs. Analyzing the role of FG richness relative to species richness was pioneered by research using the biodiversity experiments carried out at Cedar Creek in the USA (Tilman *et al.* 1997a) and at the BIODEPTH sites in Europe (Hector *et al.* 1999; Spehn *et al.* 2005). Other biodiversity experiments focused on the role of FG richness relative to FG composition (Hooper & Vitousek 1997; Symstad & Tilman 2001; Hooper & Dukes 2004; Gross *et al.* 2007). However, in these previous experiments, it was difficult to distinguish effects of FG richness or species richness from an increased probability of including a particular FG or species in a community. It was therefore suggested that e.g. legume presence was in fact the hidden driver of primary productivity in these experiments, not species richness or FG richness *per se* (Huston *et al.* 2000; Huston & McBride 2002; Mulder *et al.* 2002, but see Van Ruijven & Berendse 2005). In contrast to previous experiments, a confounding between species richness, FG richness and FG composition was minimized in the "Jena Experiment" (Roscher *et al.* 2004). Figure A1 illustrates this improved design by contrasting exemplarily the relationship

between species richness, sown proportion of legumes and number of experimental communities in BIODEPTH and the Jena Experiment.

We applied the additive partitioning method of Loreau and Hector (2001) to quantify the contributions of complementarity (including facilitation) vs. selection (including sampling and dominance) to net effects of species diversity. This method enabled us to examine how these effects changed over time. However, to cope with the downsides of this method such as the difficult ecological interpretation of the resulting indices (Petchey 2003; Fox 2005; Zhang & Zhang 2007) and its dependency on the performance of species in monoculture as exclusive reference point (Adler & Bradford 2002; Fox 2006; Schmid *et al.* 2008), we additionally performed a replacement series analysis (De Wit 1960; Connolly 1986) to analyze whether mixtures perform better than the average of the component monocultures (overyielding) or than any of the component monocultures (transgressive overyielding, Trenbath 1974). This approach takes into account that the relative abundance of species or FGs is expected to have a significant effect on ecosystem functioning (Mulder *et al.* 2004; Hooper *et al.* 2005; Kirwan *et al.* 2007).

The Jena Experiment is a large-scale biodiversity experiment that was specifically designed to disentangle the effects of species richness, FG richness, presence of particular FGs and proportional abundance (hereafter proportions) of FGs on ecosystem processes and thus help to elucidate the underlying mechanisms of biodiversity effects (Roscher *et al.* 2004). It includes four FGs in proportions ranging from 0 % to 100 % at all species richness levels up to at least 8 species (Table 1), allowing the separation of the effects of the presence and proportions of individual FGs from each other and from species richness effects. Furthermore, the Jena Experiment fulfills the conditions for the additive partitioning method (as all species were grown in monocultures) as well as for the replacement series approach (using proportional abundances of functional groups instead of species proportions on the x-axis).

Previous research has shown that biodiversity effects as well as the underlying mechanisms may change over time (Tilman *et al.* 2001; Hooper & Dukes 2004; Spehn *et al.* 2005; Van Ruijven & Berendse 2005; Cardinale *et al.* 2007; Fargione *et al.* 2007; Weis *et al.* 2007). Therefore, only studies comprising multiple years may result in reliable conclusions about biodiversity effects. Using data of a 6-year grassland experiment, we asked the following questions: (1) what are the effects of species richness, FG richness, presence of particular FGs and of their proportions on aboveground community biomass and which mechanisms underlie these effects? (2) What are the temporal dynamics in the effects of the different diversity components as well as in the possibly responsible mechanisms?

Methods

STUDY AREA & EXPERIMENTAL DESIGN

The field site of the Jena Experiment encompasses approx. 10 ha of former agricultural land in the floodplain of the river Saale near Jena (Germany, 50°55' N, 11°35' E, 130 m altitude). The area around Jena is characterized by a mean annual air temperature of 9.3 °C, and a mean annual precipitation of 587 mm (Kluge & Müller-Westermeier 2000). The soil consists of sandy loam in the vicinity of the river which gradually changes to silty clay with increasing distance from the river.

In May 2002, 78 plant assemblages of common Central European grassland species were sown with a total of 1000 viable seeds per m² on plots of 20 x 20 m that had been kept fallow in the year before sowing, harrowed bimonthly and treated with glyphosate (Roundup, Monsanto company, St. Louis, Missouri USA) in July 2001. Species compositions were determined by constrained random selection from a pool of 60 species. Based on a cluster analysis of ecological and morphological traits, these 60 target species had been assigned to four FGs: 16 grasses, 12 small herbs, 20 tall herbs and 12 legumes. In mixtures, all species were sown with equal proportions and in plots with more than one FG all FGs were sown as evenly as possible (Roscher *et al.* 2004).

Table 1 shows the sown levels of species richness and FG richness as well as the sown proportions of each FG at the different diversity levels. Species richness, FG richness and the presence of the FGs were varied as orthogonally as possible. However, there were not enough legumes and small herbs in the overall species pool to assemble them in mixtures with 16 species of the same FG. Each FG was sown in four monocultures, six 2-species mixtures, ten 4-species mixtures, ten 8-species mixtures and nine or ten 16-species mixtures which resulted in the presence of each FG on 39 (legumes and small herbs) or 40 (tall herbs and grasses) of the 78 plots. For the FG richness levels of 1, 3 and 4, all possible combinations of FGs were sown. For the level of 2 FGs, four out of six possible combinations were randomly selected. This procedure resulted in 13 different combinations of the four FGs sown at the different species richness levels.

Additionally, 120 monoculture plots of 3.5 x 3.5 m were established (two replicates per species). All experimental plots were maintained without fertilizer application and mown twice a year (in early June and early September). Species occurring on plots where they had not been sown were removed during biannual weeding campaigns (at the beginning of the growing season and after the first mowing). Weeding was mainly done by hand; herbicides were used where target species composition allowed their application (herbicides against

dicots in pure grass communities and against grasses on plots with herbs only). Empirical data showed that the application of herbicides did not affect the relationship between biodiversity and aboveground community biomass: on each of our grassland plots, a small subplot was only weeded and never treated with herbicides. These subplots showed the same biodiversity–productivity relationship as observed on the rest of the plots (Roscher *et al.* 2009b). The weeding treatment however might have decreased or increased the biodiversity–productivity relationship to some extent because low-diversity plots had to be weeded more intensively than high-diversity plots (Weigelt, unpublished data). Weeding could have been beneficial for the target species by creating more space and loosening the soil or it could have hampered the recruitment of target species if their seedlings were damaged. We do not know if the potential positive or negative effects prevailed but recognize these confounding possibilities as a caveat of our study.

The field site was divided into four blocks to account for altering soil and water conditions. Mixtures and monocultures of both plot sizes were distributed in nearly equal shares across all four blocks. Weeding, mowing and herbicide application were completed blockwise in rotating order.

SAMPLING

Aboveground community biomass was harvested twice a year (during peak standing biomass in late May and in late August) from 2003–2007 on all experimental plots (78 large plots and 120 small monocultures). This was done by clipping the vegetation at 3 cm above ground in four (in May 2005 and August 2007 only three) rectangles of 0.2 x 0.5 m per large plot and in two rectangles of 0.2 x 0.5 m per small monoculture. The location of these rectangles was assigned prior to each harvest by random selection of coordinates within the inner area of the plots (at least 3 m away from the plot margins in the large plots and within the inner 2 x 2 m area in the small monocultures, respectively). The positions of the rectangles within large and small plots, respectively, were identical for all plots at a particular harvest. The harvested biomass was sorted into target species (species sown at the particular plot) and dried at 70 °C for at least 48 h. Species not sown in a particular plot as well as detached dead plant material were removed before drying. In August 2004, the harvested biomass samples were not sorted into species (they were only sorted into legumes and non-legumes). Therefore, analyses requiring species-specific biomass data (e.g. additive partitioning) were restricted to the years 2003 and 2005–2007.

ESTABLISHMENT OF THE EXPERIMENTAL GRADIENT

The number of established target species was recorded twice a year in an area of 9 m² per large plot. Additionally, the number of established target species was recorded throughout the growing season in 2005–2007 on an area of approx. 180 m² (the inner area of the plots). The strong correlation between the number of sown species and the number of established target species ($R^2 > 0.9$ in all years) verified the successful establishment of the species richness gradient (Table 2). In 2006, one large monoculture (*Bellis perennis*) did not produce any aboveground community biomass and we excluded this data point from all analyses.

EFFECTS OF SPECIES RICHNESS AND FG COMPOSITION

Aboveground biomass at the time of the harvests was calculated for each experimental community as the mean of the sampled rectangles per plot. Annual aboveground community biomass (hereafter community biomass) was calculated as the sum of the two harvests per year (data from the May harvest in 2003 were previously analyzed in Roscher *et al.* (2005)). We used repeated-measures analysis of variance (ANOVA) with sequential sums of squares to assess the effects of species richness and FG composition on community biomass (Schmid *et al.* 2002a). The model terms were fitted in two sequences to account for the remaining dependency between species richness and FG composition. In model 1, species richness was fitted prior to FG composition and we decomposed the variation due to FG composition into a contrast for FG richness and residual FG composition (Table 3 and Table A1). In model 2, FG composition was fitted prior to species richness and we decomposed the variation due to FG composition into contrasts for the presence of the particular FGs and their interactions (Table 4 and Table A2). For the latter purpose, we substituted the single variable FG composition that contained the 13 sown combinations of the four FGs by four variables that coded for the presence of each of the four FGs and fitted their main effects (four terms) as well as 2- (6 terms) and 3-way (2 terms) interactions. For the within-plot analyses, the 2- and 3-way interactions were aggregated into a single term (Green & Tukey 1960). The order of the FG main effects corresponded to their effect sizes if fitted individually in a simplified year-specific model that contained the focal FG, species richness and the interaction between these two variables in this order (see Fig. A3).

EFFECTS OF FG PROPORTIONS (REPLACEMENT SERIES APPROACH)

We categorized the 78 large plots into five classes (77 plots in 2006, because the *B. perennis* monoculture was excluded). Plots where the focal FG was absent formed one class

(proportional abundance of the focal FG (PFG) = 0) and plots where the entire biomass was produced by the focal FG formed another class (PFG = 1). The remaining plots were sorted into those where the focal FG contributed less than one third ($0 < PFG < 0.33$), between one and two thirds ($0.33 \leq PFG < 0.67$) and more than two thirds ($0.67 \leq PFG < 1$) to community biomass. We considered each FG as the focal FG at a time and analyzed FG biomass and community biomass as a function of the five classes of FG-proportions (Fig. 2). This analysis corresponds to the replacement series approach introduced by de Wit (1960) that was later used in plant competition experiments (Harper 1977; Connolly 1986; Jolliffe 2000).

We performed an additional analysis in which we corrected the biomass values for the species richness of the communities. To this end, we fitted a simple linear model including the logarithm of species richness as explanatory variable to the biomass data of each year. The corrected values were then calculated as the sum of the mean biomass per year and the residuals obtained by the respective year-specific model. After having accounted for species richness in this way, we performed the replacement series analyses as described above.

ADDITIVE PARTITIONING

We used the additive partitioning method of Loreau and Hector (2001) to calculate for every plot the net biodiversity effect (NE) in all years and the complementarity effect (CE) and selection effect (SE) in the years 2003 and 2005–2007. All effects were calculated using the average between the annual biomass of the two small monocultures per species as monoculture biomass of the respective species. If a species failed to establish in both monocultures at both harvests per year it was excluded from the set of target species also in corresponding mixtures in that particular year. In 2003, two 2-species mixtures contained a species that had not established in monoculture and NE, CE and SE could therefore not be determined for these two plots in 2003. In addition, we excluded two plots in 2005 and one plot in 2006 because their transformed CE and SE fell more than 3 times the interquartile range below or above the first or third quartile, respectively. Following a conservative rule, we considered these values as outliers (Hoaglin *et al.* 1986). NE, CE and SE were analyzed with similar models as community biomass (Tables A1 and A2). To improve the normality of the error distribution, the absolute values for NE, CE and SE were square root transformed and the result was multiplied by –1 if the original value was negative.

The recently proposed modification of the additive partitioning method by Fox (2005) yielded essentially the same results as the method of Loreau and Hector (2001): the “trait dependent complementarity effect” (TDCE, a component of SE) was 0.56 ± 0.94 and not

significantly different from zero (P = 0.234). Therefore, we present only the results obtained by the 2-fold partitioning (Loreau & Hector 2001).

ROBUSTNESS OF SPECIES RICHNESS–COMMUNITY BIOMASS RELATIONSHIP

We analyzed the robustness of our results exemplarily for the relationship between sown species richness and community biomass (as assessed using model 1) by restricting its assessment to a subset of data points derived from experimental communities with a specified minimum of vegetation cover. Mean vegetation cover of the target communities was calculated as the average of two cover estimates per year, measured on an area of 9 m² on each plot at the times of the biomass harvests. We included a data point in the analysis if it represented a target community whose mean vegetation cover exceeded a threshold varying from > 0 % to > 95 % cover. Each community was judged independently in every year, i.e., if a community produced a data point below the threshold in one year its remaining data points for the other years could still be included in the analysis. The full data set contained 389 data points (derived from all 78 plots in five years minus the *B. perennis* monoculture in 2006).

This analysis showed that the positive species richness–community biomass relationship (as presented in the results section, Fig. 1) was significant (P < 0.05) until less than one third of all plots were analyzed (with a vegetation cover > 92 %, Fig. A2). Only few plots had a cover of < 50 % and excluding these from the analysis had almost no effect on the relationship between species richness and community biomass. Thresholds around 70 % vegetation cover resulted in lower values for R^2 but the strength of the relationship increased again if the threshold was set higher. We think this result justifies the inclusion of all data points derived from communities with a vegetation cover > 0 in the analyses presented here.

We used the statistical software R (Version 2.6.2; http://www.r-project.org) for all calculations and statistical analyses.

Results

EFFECTS OF SPECIES RICHNESS AND FG COMPOSITION

We found a positive linear relationship between the logarithm of species richness and community biomass over the entire observation period from 2003–2007 (Fig. 1a). Mean community biomass per m² declined from 2003–2005 but then recovered again (2006 and 2007). The strength of the relationship between the logarithm of species richness and community biomass varied significantly between the years (term "Log (SR) x Year" in Table 3; level of significance $\alpha = 0.05$, same hereafter) and was stronger in the years 2006 and 2007

than in the earlier years of our study (Fig. 1a). On average, doubling the number of species increased community biomass by 91 g/m². Species richness explained 18 % of the variation in community biomass between the plots when fitted prior to FG composition (Table 3). Within a given level of species richness, FG composition strongly affected community biomass. A significant proportion of this effect was caused by increasing the number of FGs ("FG richness" in Table 3), suggesting that species were more complementary among FGs than within FGs. In addition, the particular combination of FGs played an important role independently of their number ("FG composition residuals" in Table 3). The effect of FG composition changed significantly over time.

When we did not control for differences in species richness, FG composition explained 51 % of the variation in community biomass among plots (Table 4). FG richness was responsible for almost a third of this proportion and the relationship between FG richness and community biomass was temporally stable (Table 4, Fig. 1b). On average, adding one FG to a community increased community biomass by 103 g/m². The biomass of communities containing the same number of FGs was significantly affected by the identity of the FGs present ("FG composition residuals" in Table 4). In particular, legumes and tall herbs had significant positive effects. The effect of legumes on community biomass changed over time and was especially strong in 2006 (Table 4, Fig. A3). In some years, legumes also affected the strength of the relationship between species richness and community biomass ("Presence legumes x log (SR) x Year" in Table 4). The effect of tall herbs was strongest in 2003 and not any longer observed in 2006 and 2007 (Table 4, Fig. A3). Small herbs showed a tendency to reduce community biomass but this effect was only significant in 2004 (Table 4, Fig. A3). Grasses slightly enhanced community biomass in 2003 (Fig. A3) but averaged over all years their effect was not significant (Table 4). The effects of the presence of particular FGs and of species richness were additive as none of the corresponding interactions in model 2 or in the analyses for Fig. A3 were significant. These interactions were therefore subsumed under the term "FG composition x log (SR)" in Table 4 and not displayed in Fig. A3. Among communities of equal FG composition those with more species produced more biomass ("species richness" in Table 4).

EFFECTS OF FG PROPORTIONS (REPLACEMENT SERIES APPROACH)

If mixed with species from other FGs, any of our four FGs could enhance the absolute biomass of a community beyond the biomass of communities where its proportion was either 0 % or 100 % (i.e., some inner bars were always higher than outer bars in Fig. 2). Such

transgressive overyielding (Trenbath 1974) occurred for all four FGs in all years at least at one and often at several of the mixing ratios. When the focal FG had an abundance of less than 33 %, the sum of the biomass of the remaining FGs (white part of bars in Fig. 2) was nearly always higher as the total biomass of these FGs alone (exceptions: legumes in 2003, small herbs 2003 and 2005). In other words, the relative yield (i.e., biomass of a species in mixture divided by its biomass in monoculture, see De Wit 1960; Harper 1977; Jolliffe 2000) of the non-focal FGs was > 1, indicating facilitation of the remaining FGs by the focal FG. The relative yield of the focal FG (grey part of the bars in Fig. 2), was also often > 1 if the proportion of the focal FG was larger than 67 % (legumes in 2007, tall herbs in 2003 and 2007, small herbs in 2003, 2005 and 2007 and grasses in 2003 and 2005). This indicated that also the focal FG benefited from facilitation. The degree of transgressive overyielding between FGs was relatively constant during the observation period.

Similar results were obtained after having accounted for the number of species within the communities (not shown).

ADDITIVE PARTITIONING

Averaged over all species richness levels and all years, the net biodiversity effect NE and its components CE and SE were significantly positive (192 ± 17 g/m², 135 ± 17 g/m² and 18 ± 7 g/m) but all three effects changed over time (Tables A1 and A2). While NE decreased until 2005 and increased thereafter, CE increased and SE decreased continuously over time (Fig. 3). NE and CE were positively related to species richness in communities irrespective of whether the communities were of the same or of different FG compositions (Tables A1a and A2a for NE; A1b and A2b for CE). When fitted prior to species richness, FG composition accounted for more than half of the variation in NE and CE among plots (Tables A2a and A2b). FG richness was responsible for more than a third (NE) or more than half (CE) of this amount. Replacing the FG richness contrast with contrasts for the presence of particular FGs and their interactions revealed a strong positive impact of legumes and a positive effect of tall herbs on NE and CE. The effect of legumes on NE and CE occurred during the entire observation period (Tables A2a and A2b). The positive effect of tall herbs on NE decreased significantly over time (Table A2a), whereas the positive effect of tall herbs on CE remained (Table A2b). SE was not affected by species richness and only marginally affected by FG composition in some years. An initially positive effect of tall herbs on SE decreased significantly over time (Tables A1c and A2c).

Discussion

EFFCTS OF DIVERSITY COMPONENTS ON COMMUNITY BIOMASS

We identified strong positive effects of the two richness components (species richness and FG richness) and of the presence of two particular FGs, legumes and tall herbs, on community biomass, NE and CE. It is often assumed that effects of species richness should be weaker than effects of FG richness (Hooper *et al.* 2005; Jiang *et al.* 2007). However, this was not supported by our results. In previous experiments, the two richness components were usually more strongly confounded with FG composition than in the Jena Experiment and effects of species richness and especially of FG richness could therefore be interpreted as effects caused by an increased probability for the inclusion of legumes at higher richness levels (Spehn *et al.* 2005). In our experiment, this confounding was minimized (see Fig. A1) and species richness remained highly significant when we corrected for all effects that were potentially due to the presence of particular FGs or their interactions. Thus, our results demonstrate that increasing species richness without changing FG composition has a positive effect on community biomass and support the conclusions of Reich *et al.* (2004) and Lanta & Lepš (2007) in that species within FGs are not completely redundant in their functions. Nevertheless, if the effect of species richness was measured across different FG compositions, its effect was about three times as large as within a particular combination of FGs (compare Table 3 with Table 4). This suggests that the greater differences between species across as opposed to within FGs resulted in increased complementarity and positive species richness effects when different FGs were mixed (Tilman *et al.* 1997b; Loreau 1998).

Of our four FGs, legumes had the strongest and generally positive effects on community biomass and NE. This was mainly due to positive interactions between legumes and species belonging to other FGs (as seen in Fig. 2 and in the positive effect of legume presence on CE, Table A2b). Disproportionate contributions of legume biomass to community biomass were less important (no significant effect of legume presence on SE, Table A2c). Strong positive effects of legumes on community biomass have been found in other biodiversity experiments (Tilman *et al.* 1997a; Hector *et al.* 1999; Tilman *et al.* 2001; Mulder *et al.* 2002; Hille Ris Lambers *et al.* 2004; Spehn *et al.* 2005) which may be explained by the improved nitrogen availability on legume-containing plots promoting complementary resource use or facilitation (Spehn *et al.* 2002; Fridley 2003; Dimitrakopoulos & Schmid 2004; Oelmann *et al.* 2007b; Temperton *et al.* 2007).

Tall herbs increased community biomass and NE partly via complementarity (as seen in Fig. 2 and in the positive effect of tall herb presence on CE, Table A2b) and partly via

disproportionate contributions of tall herb biomass to community biomass (as seen in the positive effect of tall herb presence on SE, Table A2c). Tall herbs were generally characterized by a medium or tall stature but were rather variable with regard to other traits (Roscher *et al.* 2004). While their positive effect on SE was likely related to their tall growth, their contribution to community biomass via complementarity could have been the result of various mechanisms that await further clarification.

Grasses and small herbs had minor effects on community biomass. While the minor effects of small herbs on community biomass were not surprising, we had expected a stronger impact of grasses as they had pronounced effects on other ecosystem functions in the Jena Experiment: grasses decreased individual plant performance (Scherber *et al.* 2006; Mwangi *et al.* 2007), increased invasion resistance (Roscher *et al.* 2009a), changed nitrogen and phosphorus fluxes (Oelmann *et al.* 2007a; Oelmann *et al.* 2007b) and affected the soil fauna (Milcu *et al.* 2006).

The replacement series analyses showed that any of our FGs could generate a positive biodiversity effect (see Fig. 2). In agreement with our remaining analyses we found the largest effects for legumes and tall herbs. However, small herbs and grasses generated positive effects as well if their proportions were low. Several mechanisms could be the drivers of such positive interactions not necessarily involving legumes, e.g. increased light- and nutrient-use efficiency, favorable alteration of micro-climatic conditions, or beneficial changes in soil properties (Callaway 1997; Van Ruijven & Berendse 2005; Callaway 2007; Daßler *et al.* 2008).

If the mixing ratio between the focal FG and the non-focal FGs fell within a particular range, community biomass was higher than if the focal FG or the non-focal FG grew alone. Therefore, mixed assemblages (containing the focal FG as well as non-focal FGs) could transgressively overyield pure assemblages (containing only the focal FG or the non-focal FGs). Transgressive overyielding is generally regarded as a conservative test for complementarity because the sampling effect alone cannot result in mixtures producing more biomass than any of the component monocultures (Huston *et al.* 2000; Tilman *et al.* 2001). We could further rule out sampling as the main mechanism for increasing community biomass in all cases in which the relative yield was > 1. Here, the beneficial effect of mixing different FGs was not only apparent for the total community but also for the respective fraction illustrating the possibility that community biomass is enhanced via increasing diversity even if the biomass of the added species is not considered for the outcome.

Relative yields > 1 are particularly informative because they reveal that facilitation and not only reduced resource competition (complementarity in the strict sense) contributed to the positive biodiversity effect (Schmid *et al.* 2002b). So far, only few experimental studies have been reported that achieved to differentiate between these two mechanisms (Caldeira *et al.* 2001; Mulder *et al.* 2001; see also the discussion of this issue in Callaway 2007). To our knowledge, relative yields > 1 were only once demonstrated in a similar way in mixtures of two species (Weiner 1980) but never in mixtures of multiple FGs.

Transgressive overyielding is thought to be rather the exception than the rule (Cardinale *et al.* 2006; but see Kirwan *et al.* 2007). However, it has been shown that the calculation of a transgressive overyielding index involves a sample bias (Schmid *et al.* 2008) of which our results are unaffected. We showed that transgressive overyielding occurred for all four focal FGs in all years. This remarkable consistency suggests that transgressive overyielding may be more common than previously estimated.

The lack of significant 2- and 3-way interactions between the presences of the individual FGs indicates that the FGs exerted their effects on community biomass without compromising the effect of the other FGs present. Mixing legumes and tall herbs therefore led to a double positive effect. Similarly, the additiveness of the effects of the presence of particular FGs and of species richness as well as the fact that any of our FGs could generate transgressive overyielding if present at a particular proportion demonstrates that the combined contributions of different FGs in many cases increased community biomass even further than the presence of a single FG.

TEMPORAL DYNAMICS IN BIODIVERSITY EFFECTS

In the past, analyses of biodiversity–ecosystem functioning relationships that used data of multiple years produced ambiguous results. The effect of biodiversity was observed to either increase (Tilman *et al.* 2001; Mulder *et al.* 2002; Hooper & Dukes 2004; Spehn *et al.* 2005; Van Ruijven & Berendse 2005; Fargione *et al.* 2007), or decrease over time (Bell *et al.* 2005), or to show complex temporal dynamics (Weis *et al.* 2007). In our experiment, the effects of species richness and FG richness on community biomass as well as NE were positive throughout the entire observation period and the effect of species richness increased with time. We conclude that biodiversity effects are not a transient phenomenon only found during plant community establishment and may instead increase over time.

The increasing CE but decreasing SE suggested that, over time, positive interactions between multiple species or FGs became relatively more important for the generation of

biodiversity effects than disproportionate effects of single species or FGs (see Fig. 3). A decrease in the average SE can have several reasons: either species in mixture approach more and more their expected abundances, or the variance between the monocultures of the component species declines over time, or the number of negative values for SE increases in the sample. While the first two of these alternatives are incompatible with our observation that the variance in SE increased between 2003 and 2005, the third explanation seems plausible as the number of plots with a negative SE increased indeed during that period (not shown).

Negative selection effects have been reported from several other studies (Špaèková & Lepš 2001; Hooper & Dukes 2004; Cardinale *et al.* 2007; Jiang 2007) and result either from species with higher-than-average biomass in monoculture that perform relatively poorly in mixture (Hooper & Dukes 2004) or from species with a lower-than-average biomass in monoculture that are more abundant in mixture than expected (Cardinale *et al.* 2007). As we observed a strong increase in CE, the likely cause for a higher number of negative SE values was the increasing promotion of the growth of species in mixture that performed poorly in monoculture. This conclusion supports previous findings (Hille Ris Lambers *et al.* 2004; Fargione *et al.* 2007) in that the performance of a species in monoculture does not necessarily predict its competitive abilities in mixtures and highlights once more that effect sizes calculated by the additive partitioning method according to Loreau and Hector (2001) need to be interpreted with care.

In summary, the continuously positive effects of species richness and FG richness and the positive values for NE demonstrate that the biomass of mixtures exceeded their expected yields based on their component monocultures' performances in all years. In agreement with a recent meta-analysis showing that biodiversity effects resulted most often from a combination of multi-species complementarity and species-specific selection effects (Cardinale *et al.* 2007) we could show that both mechanisms played a role in the Jena Experiment. Nevertheless, the evidence for facilitation and transgressive overyielding was strong and the strength and relative importance of complementarity increased over time.

Conclusions

Aboveground biomass production in plant communities is affected by several components of plant biodiversity such as species richness, FG richness, presence of particular FGs and their proportions. Therefore, the loss of species from ecosystems is likely to result in reductions of ecosystem functions, irrespective of the nature of the diversity component that is lost. Species

within FGs are not necessarily redundant with regard to community biomass and effects of different diversity components may be additive. Mixing species of different FGs can lead to strong transgressive overyielding and additive and facilitative effects between species and FGs increase over time. We suggest that methods presently not commonly used in biodiversity research, such as the replacement series analysis, and the consideration of diversity components other than species richness can broaden our understanding of the consequences of changing biodiversity.

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Chapter references

Aarssen L. W. (1997). High productivity in grassland ecosystems: effected by species diversity or productive species? *Oikos*, **80**, 183-184.

Adler P. B. & Bradford J. B. (2002). Compensation: an alternative method for analyzing diversity-productivity experiments. *Oikos*, **96**, 411-420.

Balvanera P., Pfisterer A. B., Buchmann N., He J.-S., Nakashizuka T., Raffaelli D. & Schmid B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, **9**, 1-11.

Bell T., Newman J. A., Silverman B. W., Turner S. L. & Lilley A. K. (2005). The contribution of species richness and composition to bacterial services. *Nature*, **436**, 1157-1160.

Caldeira M. C., Ryel R. J., Lawton J. H. & Pereira J. S. (2001). Mechanisms of positive biodiversity-production relationships: insights provided by □13C analysis in experimental Mediterranean grassland plots. *Ecology Letters*, **4**, 439-443.

Callaway R. M. (1997). Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia*, **112**, 143-149.

Callaway R. M. (2007). *Positive interactions and interdependence in plant communities*. Springer, Dordrecht.

Cardinale B. J., Srivastava D. S., Duffy J. E., Wright J. P., Downing A. L., Sankaran M. & Jouseau C. (2006). Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, **443**, 989-992.

Cardinale B. J., Wrigh J. P., Cadotte M. W., Carroll I. T., Hector A., Srivastava D. S., Loreau M. & Weis J. J. (2007). Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences*, **104**, 18123-18128.

Chapin F. S., Zavaleta E. S., Eviner V. T., Naylor R. L., Vitousek P. M., Reynolds H. L., Hooper D. U., Lavorel S., Sala O. E., Hobbie S. E., Mack M. C. & Díaz S. (2000). Consequences of changing biodiversity. *Nature*, **405**, 234-242.

Connolly J. (1986). On difficulties with replacement-series methodology in mixture experiments. *Journal of Applied Ecology*, **23**, 125-137.

Daßler A., Roscher C., Temperton V. M., Schumacher J. & Schulze E.-D. (2008). Adaptive survival mechanisms and growth limitations of small-stature herb species across a plant diversity gradient. *Plant Biology*, **10**, 573-587.

De Wit C. T. (1960). On competition. *Verslagen Landbouwkundige Onderzoekingen*, **66**, 1-82.

Díaz S. & Cabido M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, **16**, 646-655.

Díaz S., Fargione J., Chapin F. S. & Tilman D. (2006). Biodiversity loss threatens human well-being. *Plos Biology*, **4**, 1300-1305.

Dimitrakopoulos P. G. & Schmid B. (2004). Biodiversity effects increase linearly with biotope space. *Ecology Letters*, **7**, 574-583.

Fargione J., Tilman D., Dybzinski R., Hille Ris Lambers J., Clark C., Harpole W. S., Knops J. M. H., Reich P. B. & Loreau M. (2007). From selection to complementarity: shifts in the causes of biodiversity-productivity relationships in a long-term biodiversity experiment. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **274**, 871-876.

Fox J. W. (2005). Interpreting the 'selection effect' of biodiversity on ecosystem function. *Ecology Letters*, **8**, 846-856.

Fox J. W. (2006). Using the Price Equation to partition the effects of biodiversity loss on ecosystem function. *Ecology*, **87**, 2687-2696.

Fridley J. D. (2003). Diversity effects on production in different light and fertility environments: an experiment with communities of annual plants. *Journal of Ecology*, **91**, 396-406.

Green B. F. & Tukey J. W. (1960). Complex analyses of variance: general problems. *Psychometrika*, **25**, 127-152.

Gross N., Suding K. N., Lavorel S. & Roumet C. (2007). Complementarity as a mechanism of coexistence between functional groups of grasses. *Journal of Ecology*, **95**, 1296-1305.

Harper J. L. (1977). *Population biology of plants*. Academic Press, London, UK.

Hector A., Schmid B., Beierkuhnlein C., Caldeira M. C., Diemer M., Dimitrakopoulos P. G., Finn J. A., Freitas H., Giller P. S., Good J., Harris R., Högberg P., Huss-Danell K., Joshi J., Jumpponen A., Körner C., Leadley P. W., Loreau M., Minns A., Mulder C. P. H., O'Donovan G., Otway S. J., Pereira J. S., Prinz A., Read D. J., Scherer-Lorenzen M., Schulze E.-D., Siamantziouras A.-S. D., Spehn E. M., Terry A. C., Troumbis A. Y., Woodward F. I., Yachi S. & Lawton J. H. (1999). Plant diversity and productivity experiments in European grasslands. *Science*, **286**, 1123-1127.

Hille Ris Lambers J., Harpole S. W., Tilman D., Knops J. & Reich P. B. (2004). Mechanisms responsible for the positive diversity-productivity relationship in Minnesota grasslands. *Ecology Letters*, **7**, 661-668.

Hoaglin D. C., Iglewicz B. & Tukey J. W. (1986). Performance of some resistant rules for outlier labeling. *Journal of the American Statistical Association*, **81**, 991-999.

Hooper D. U. & Vitousek P. M. (1997). The effects of plant composition and diversity on ecosystem processes. *Science*, **277**, 1302-1305.

Hooper D. U., Solan M., Symstad A., Díaz S., Gessner M. O., Buchmann N., Degrange V., Grime P., Hulot F., Mermillod-Blondin F., Roy J., Spehn E. & Van Peer L. (2002). Species diversity, functional diversity, and ecosystem functioning. In: *Biodiversity and ecosystem functioning: Synthesis and Perspectives* (eds. Loreau M., Naeem S. & Inchausti P.). Oxford University Press New York, pp. 195-208.

Hooper D. U. & Dukes J. S. (2004). Overyielding among plant functional groups in a long-term experiment. *Ecology Letters*, **7**, 95-105.

Hooper D. U., Chapin F. S., Ewel J. J., Hector A., Inchausti P., Lavorel S., Lawton J. H., Lodge D. M., Loreau M., Naeem S., Schmid B., Setälä H., Symstad A. J., Vandermeer J. & Wardle D. A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3-35.

Huston M. A. (1997). Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, **110**, 449-460.

Huston M. A., Aarssen L. W., Austin M. P., Cade B. S., Fridley J. D., Garnier E., Grime J. P., Hodgson J., Lauenroth W. K., Thompson K., Vandermeer J. H. & Wardle D. A. (2000). No consistent effect of plant diversity on productivity. *Science*, **289**, 1255a.

Huston M. A. & McBride A. C. (2002). Evaluating the relative strengths of biotic versus abiotic controls on ecosystem processes. In: *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives* (eds. Loreau M., Naeem S. & Inchausti P.). Oxford University Press Oxford, pp. 47-60.

Jiang L. (2007). Negative selection effects suppress relationships between bacterial diversity and ecosystem functioning. *Ecology*, **88**, 1075-1085.

Jiang X. L., Zhang W. G. & Wang G. (2007). Effects of different components of diversity on productivity in artificial plant communities. *Ecological Research*, **22**, 629-634.

Jolliffe P. A. (2000). The replacement series. *Journal of Ecology*, **88**, 371-385.

Kirwan L., Lüscher A., Sebastia M. T., Finn J. A., Collins R. P., Porqueddu C., Helgadottir A., Baadshaug O. H., Brophy C., Coran C., Dalmannsdottir S., Delgado I., Elgersma A., Fothergill M., Frankow-Lindberg B. E., Golinski P., Grieu P., Gustavsson A. M., Hoglind M., Huguenin-Elie O., Iliadis C., Jorgensen M., Kadziuliene Z., Karyotis T., Lunnan T., Malengier M., Maltoni S., Meyer V., Nyfeler D., Nykanen-Kurki P., Parente J., Smit H. J., Thumm U. & Connolly J. (2007). Evenness drives consistent diversity effects in intensive grassland systems across 28 European sites. *Journal of Ecology*, **95**, 530-539.

Kluge G. & Müller-Westermeier G. (2000). *Das Klima ausgewählter Orte der Bundesrepublik Deutschland: Jena*. Deutscher Wetterdienst, Offenbach/Main.

Lanta V. & Lepš J. (2007). Effects of species and functional group richness on production in two fertility environments: an experiment with communities of perennial plants. *Acta Oecologica*, **32**, 93-103.

Loreau M. (1998). Biodiversity and ecosystem functioning: a mechanistic model. *Proceedings of the National Academy of Sciences*, **95**, 5632-5636.

Loreau M. & Hector A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, **412**, 72-76.

Milcu A., Partsch S., Langel R. & Scheu S. (2006). The response of decomposers (earthworms, springtails and microorganisms) to variations in species and functional group diversity of plants. *Oikos*, **112**, 513-524.

Mulder C. P. H., Uliassi D. D. & Doak D. F. (2001). Physical stress and diversity-productivity relationships: the role of positive interactions. *Proceedings of the National Academy of Sciences*, **98**, 6704-6708.

Mulder C. P. H., Jumpponen A., Högberg P. & Huss-Danell K. (2002). How plant diversity and legumes affect nitrogen dynamics in experimental grassland communities. *Oecologia*, **133**, 412-421.

Mulder C. P. H., Bazeley-White E., Dimitrakopoulos P. G., Hector A., Scherer-Lorenzen M. & Schmid B. (2004). Species evenness and productivity in experimental plant communities. *Oikos*, **107**, 50-63.

Mwangi P. N., Schmitz M., Scherber C., Roscher C., Schumacher J., Scherer-Lorenzen M., Weisser W. W. & Schmid B. (2007). Niche pre-emption increases with species richness in experimental plant communities. *Journal of Ecology*, **95**, 65-78.

Oelmann Y., Kreutziger Y., Temperton V. M., Buchmann N., Roscher C., Schumacher J., Schulze E. D., Weisser W. W. & Wilcke W. (2007a). Nitrogen and phosphorus budgets in experimental grasslands of variable diversity. *Journal of Environmental Quality*, **36**, 396-407.

Oelmann Y., Wilcke W., Temperton V. M., Buchmann N., Roscher C., Schumacher J., Schulze E. D. & Weisser W. W. (2007b). Soil and plant nitrogen pools as related to plant diversity in an experimental grassland. *Soil Science Society of America Journal*, **71**, 720-729.

Petchey O. L. (2003). Integrating methods that investigate how complementarity influences ecosystem functioning. *Oikos*, **101**, 323-330.

Reich P. B., Tilman D., Naeem S., Ellsworth D. S., Knops J., Craine J., Wedin D. & Trost J. (2004). Species and functional group diversity independently influence biomass accumulation and its response to CO2 and N. *Proceedings of the National Academy of Sciences*, **101**, 10101-10106.

Roscher C., Schumacher J., Baade J., Wilcke W., Gleixner G., Weisser W. W., Schmid B. & Schulze E.-D. (2004). The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. *Basic and Applied Ecology*, **5**, 107-121.

Roscher C., Temperton V. M., Scherer-Lorenzen M., Schmitz M., Schumacher J., Schmid B., Buchmann N., Weisser W. W. & Schulze E.-D. (2005). Overyielding in experimental grassland communities - irrespective of species pool or spatial scale. *Ecology Letters*, **8**, 419-429.

Roscher C., Beßler H., Oelmann Y., Engels C., Wilcke W. & Schulze E.-D. (2009a). Resources, recruitment limitation and invader species identity determine pattern of spontaneous invasion in experimental grasslands. *Journal of Ecology*, **97**, 32-47.

Roscher C., Temperton V. M., Buchmann N. & Schulze E.-D. (2009b). Community assembly and biomass production in regularly and never weeded experimental grasslands. *Acta Oecologia*, **35**, 206-217.

Scherber C., Milcu A., Partsch S., Scheu S. & Weisser W. W. (2006). The effects of plant diversity and insect herbivory on performance of individual plant species in experimental grassland. *Journal of Ecology*, **94**, 922-931.

Schmid B., Hector A., Huston M., Inchausti P., Nijs I., Leadley P. & Tilman D. (2002a). The design and analysis of biodiversity experiments. In: *Biodiversity and ecosystem functioning: Synthesis and Perspectives* (eds. Loreau M., Naeem S. & Inchausti P.). Oxford University Press New York, pp. 61-75.

Schmid B., Joshi J. & Schläpfer F. (2002b). Empirical evidence for biodiversity-ecosystem functioning relationships. In: *Functional consequences of biodiversity: Experimental progress and theoretical extensions* (eds. Kinzig A., Tilman D. & Pacala P.). Princeton University Press Princeton, New Jersey, pp. 120-150.

Schmid B., Hector A., Saha P. & Loreau M. (2008). Biodiversity effects and transgressive overyielding. *Journal of Plant Ecology*, **1**, 95-102.

Špaèková I. & Lepš J. (2001). Procedure for separating the selection effect from other effects in diversity-productivity relationship. *Ecology Letters*, **4**, 585-594.

Spehn E. M., Scherer-Lorenzen M., Schmid B., Hector A., Caldeira M. C., Dimitrakopoulos P. G., Finn J. A., Jumpponen A., O'Donnovan G., Pereira J. S., Schulze E. D., Troumbis A. Y. & Körner C. (2002). The role of legumes as a component of biodiversity in a cross-European study of grassland biomass nitrogen. *Oikos*, **98**, 205-218.

Spehn E. M., Hector A., Joshi J., Scherer-Lorenzen M., Schmid B., Bazeley-White E., Beierkuhnlein C., Caldeira M. C., Diemer M., Dimitrakopoulos P. G., Finn J. A., Freitas H., Giller P. S., Good J., Harris R., Högberg P., Huss-Danell K., Jumpponen A., Koricheva J., Leadley P. W., Loreau M., Minns A., Mulder C. P. H., O'Donovan G., Otway S. J., Palmborg C., Pereira J. S., Pfisterer A. B., Prinz A., Read D. J., Schulze E.-D., Siamantziouras A.-S. D., Terry A. C., Troumbis A. Y., Woodward F. I., Yachi S. & Lawton J. H. (2005). Ecosystem effects of biodiversity manipulations in European grasslands. *Ecological Monographs*, **75**, 37-63.

Symstad A. J. & Tilman D. (2001). Diversity loss, recruitment limitation, and ecosystem functioning: lessons learned from a removal experiment. *Oikos*, **92**, 424-435.

Temperton V. M., Mwangi P. N., Scherer-Lorenzen M., Schmid B. & Buchmann N. (2007). Positive interactions between nitrogen-fixing legumes and four different neighbouring species in a biodiversity experiment. *Oecologia*, **151**, 190-205.

Thomas C. D., Cameron A., Green R. E., Bakkenes M., Beaumont L. J., Collingham Y. C., Erasmus B. F. N., De Siqueira M. F., Grainger A., Hannah L., Hughes L., Huntley B., Van Jaarsveld A. S., Midgley G. F., Miles L., Ortega-Huerta M. A., Peterson A. T., Phillips O. L. & Williams S. E. (2004). Extinction risk from climate change. *Nature*, **427**, 145-148.

Tilman D., Knops J., Wedin D., Reich P., Ritchie M. & Siemann E. (1997a). The influence of functional diversity and composition on ecosystem processes. *Science*, **277**, 1300-1302.

Tilman D., Lehman C. L. & Thomson K. T. (1997b). Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences*, **94**, 1857-1861.

Tilman D., Reich P. B., Knops J., Wedin D., Mielke T. & Lehman C. (2001). Diversity and productivity in a long-term grassland experiment. *Science*, **294**, 843-845.

Trenbath B. R. (1974). Biomass productivity of mixtures. *Advances in Agronomy*, **26**, 177-210.

Van Ruijven J. & Berendse F. (2005). Diversity-productivity relationships: initial effects, long-term patterns, and underlying mechanisms. *Proceedings of the National Academy of Sciences*, **102**, 695-700.

Van Vuuren D. P., Sala O. E. & Pereira H. M. (2006). The future of vascular plant diversity under four global scenarios. *Ecology and Society*, **11**, Art. 25.

Weiner J. (1980). The effects of plant density, species proportion and potassium-phosphorus fertilization on interference between Trifolium incarnatum and Lolium multiflorum with limited nitrogen supply. *Journal of Ecology*, **68**, 969-979.

Weis J. J., Cardinale B. J., Forshay K. J. & Ives A. R. (2007). Effects of species diversity on community biomass production change over the course of succession. *Ecology*, **88**, 929-939.

Zhang Q. G. & Zhang D. Y. (2007). Consequences of individual species loss in biodiversity experiments: an essentiality index. *Acta Oecologica*, **32**, 236-242.

Table 1. Number of experimental plant communities at each level of species richness and functional group (FG) richness and the sown proportions for each FG.

Species richness	**Functional group (FG) richness**				Total no.	**Sown proportions for each FG**
	1	**2**	**3**	**4**		
	No. of experimental communities					
1	16				16	0; 1
2	8	8			16	0; 0.5; 1
4	4	4	4	4	16	0; 0.25; 0.5; 1
8	4	4	4	4	16	0; 0.25; 0.375; 0.5; 1
16	2	4	4	4	14	0; 0.25; 0.3125; 0.375; 0.5; 1*
Total no.	34	20	12	12	78	

* 1 only for grasses and tall herbs.

Table 2. Mean number of established species ("Realized") at each level of sown species richness ("Sown") in the experimental plots in the years 2003–2007. Sample area was 9 m². Numbers in brackets show the mean number of established species on an area of 180 m² in 2005–2007.

Sown	Realized 2003	Realized 2004	Realized 2005	Realized 2006	Realized 2007
1	1.0	1.0	1.0 (1.0)	0.9 (1.0)	1.0 (1.0)
2	2.0	2.0	1.9 (2.0)	2.0 (2.0)	2.0 (2.0)
4	3.6	3.9	3.7 (3.9)	3.8 (3.9)	3.8 (4.0)
8	7.4	7.4	6.9 (7.4)	6.9 (7.2)	7.3 (7.6)
16	14.3	14.5	13.7 (14.9)	13.5 (14.1)	13.4 (14.4)

Table 3. Summary of the ANOVA for aboveground community biomass from 2003–2007 (model 1 in "Methods"), using type-I sums of squares. Indented terms show the linear contrast for FG richness and its deviation from linearity (FG composition residuals). The sum of these two terms corresponds to FG composition. Year was fitted as a 5-level factor. The column % contains the proportions of explained between-plot-variation.

Source	Df	SS	MS	%	F	P
Between plots						
Block	3	1874940	624980	6	2.61	0.062
Log (species richness (SR))	**1**	**6130076**	**6130076**	**18**	**25.59**	**<0.001**
Functional group (FG) composition	**12**	**13130461**	**1094205**	**39**	**4.57**	**<0.001**
FG richness	**1**	**1091395**	**1091395**	**3**	**4.56**	**0.038**
FG composition residuals	**11**	**12039066**	**1094461**	**36**	**4.57**	**<0.001**
Log (SR) x FG composition	12	667658	55638	2	0.23	0.996
Plot residuals	*49*	*11739473*	*239581*	*35*		
Within plots						
Year	**4**	**4012604**	**1003151**		**33.36**	**<0.001**
Log (SR) x Year	**4**	**372656**	**93164**		**3.10**	**0.017**
FG composition x Year	**48**	**2156712**	**44931**		**1.49**	**0.030**
FG richness x Year	4	31293	7823		0.26	0.903
FG composition residuals x Year	**44**	**2125419**	**48305**		**1.61**	**0.015**
Log (SR) x FG composition x Year	48	1297314	27027		0.90	0.662
Residuals	*207*	*6224386*	*30069*			

Table 4. Summary of the ANOVA for aboveground community biomass from 2003–2007 (model 2 in "Methods"), using type-I sums of squares. Indented terms show two different sets of orthogonal contrasts for FG composition: (i) linear contrast for FG richness and its deviation from linearity and (ii) contrast for the presence of particular FGs and their interactions. In both cases the sum of contrast terms corresponds to FG composition. For the within plots analysis, the 2- and 3-way interactions of FGs were aggregated into the term residual FG composition. Year was fitted as a 5-level factor. The column % contains the proportions of explained between-plot-variation.

Source	Df	SS	MS	%	F	P
Between plots						
Block	3	1874940	624980	6	2.61	0.062
Functional group (FG) composition	**12**	**17015576**	**1417965**	**51**	**5.92**	**<0.001**
FG richness	**1**	**5154604**	**5154604**	**15**	**21.52**	**<0.001**
FG composition residuals	**11**	**11860973**	**1078270**	**35**	**4.50**	**<0.001**
Main effects of particular FGs	**4**	**14637569**	**3659392**	**44**	**15.27**	**<0.001**
Presence legumes	**1**	**11721881**	**11721881**	**35**	**48.93**	**<0.001**
Presence tall herbs	**1**	**1454989**	**1454989**	**4**	**6.07**	**0.017**
Presence small herbs	1	899072	899072	3	3.75	0.058
Presence grasses	1	561627	561627	2	2.34	0.132
2-way interactions between FGs*	6	1821426	303571	5	1.27	0.290
3-way interactions between FGs**	2	556581	278291	2	1.16	0.321
Log (species richness (SR))	**1**	**2244960**	**2244960**	**7**	**9.37**	**0.004**
FG composition x log (SR)	12	667656	55638	2	0.23	0.996
Plot residuals	*49*	*11739473*	*239581*	*35*		
Within plots						
Year	**4**	**4012604**	**1003151**		**33.36**	**<0.001**
FG composition x Year	**48**	**2361863**	**49205**		**2.38**	**0.002**
FG richness x Year	4	215291	53823		1.79	0.132
FG composition residuals x Year	**44**	**2146572**	**48786**		**1.62**	**0.013**
Presence of particular FGs x Year	**16**	**1504274**	**94017**		**4.54**	**<0.001**
Presence legumes x Year	**4**	**709464**	**177366**		**5.90**	**<0.001**
Presence tall herbs x Year	**4**	**346729**	**86682**		**2.88**	**0.024**
Presence small herbs x Year	4	288711	72178		2.40	0.051
Presence grasses x Year	4	159370	39842		1.33	0.262
Residual FG composition x Year	32	857589	26800		0.89	0.639
Log (SR) x Year	4	167505	41876		1.39	0.238
Presence legumes x log (SR) x Year	**4**	**386332**	**96583**		**3.21**	**0.014**
Residual FG composition x log (SR) x Year	44	910981	20704		0.69	0.929
Residuals	*207*	*6224386*	*30069*			

** includes presence legumes x tall herbs, presence legumes x small herbs, presence legumes x grasses, presence tall herbs x small herbs, presence tall herbs x grasses, presence small herbs x grasses; ** includes presence legumes x tall herbs x small herbs and presence legumes x tall herbs x grasses*

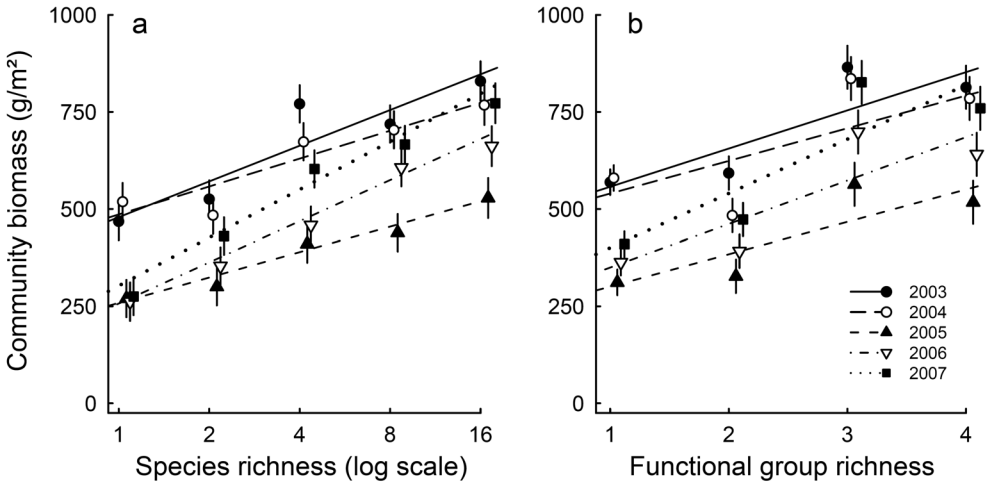

Fig. 1. Aboveground community biomass as a function of the logarithm of species richness (a) or FG richness (b) in the years 2003–2007. Symbols represent means ± 1 standard error for different years. These standard errors were obtained using the square root of the residual mean square from Table 3 as an estimate for the standard deviation of the data and dividing it by the square root of the number of replicates. Fitted lines were obtained from a simplified regression model including the logarithm of species richness as a linear contrast, year as a 5-level factor and the interaction of these variables. Symbols were slightly jittered to improve visualization.

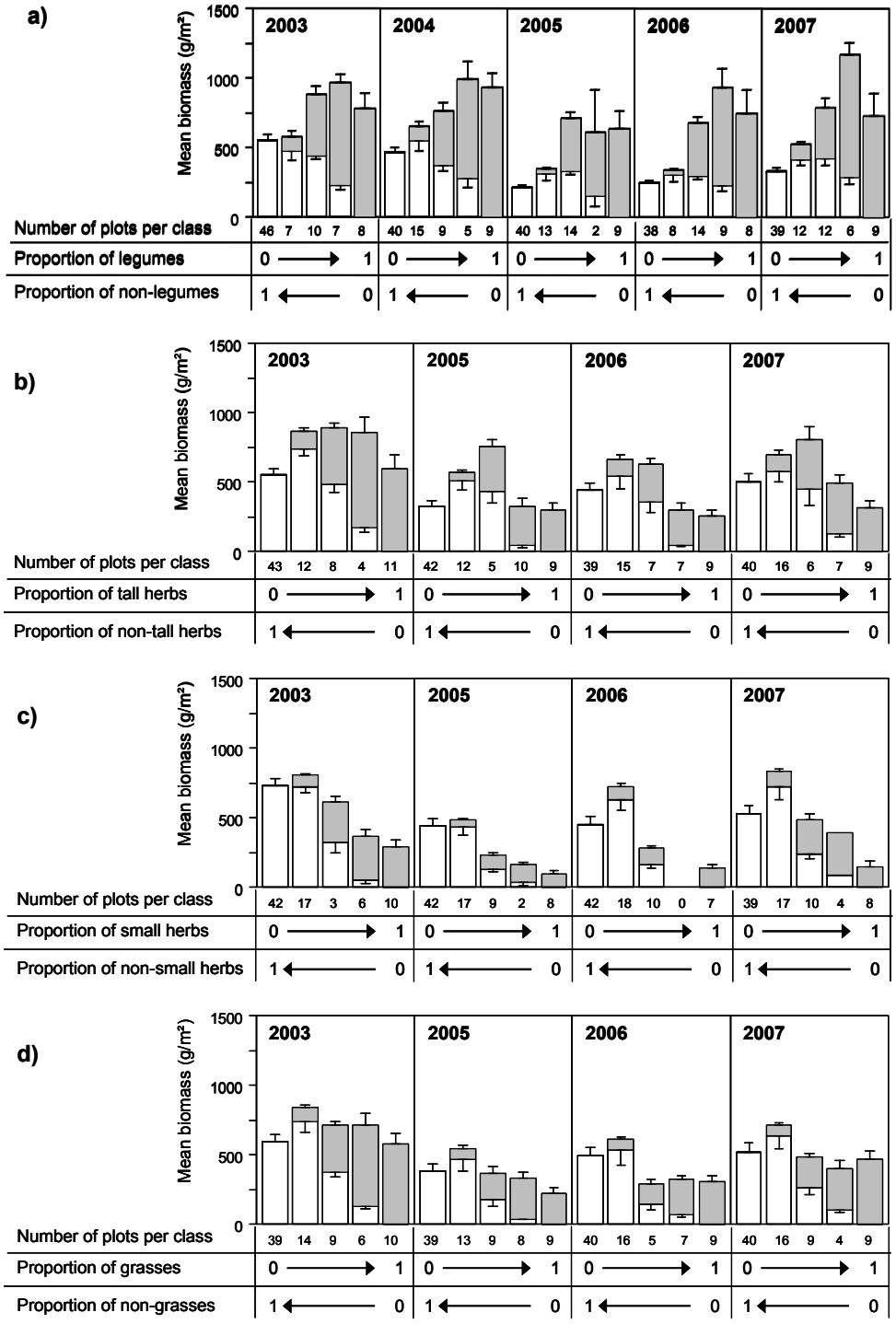

Fig. 2. Replacement series diagrams for aboveground community biomass. The x-axis represents classes of proportions of the focal FG (increasing from left to right) and the non-focal FGs (decreasing from left to right) based on relative abundance (in terms of biomass). The y-axis represents absolute aboveground biomass of the entire community, partitioned into focal FG (grey) and non-focal FGs (white). Each bar represents the mean ± 1 standard error of the corresponding proportion class. The limits of the five proportion classes, using the proportional abundances of the focal FG (PFG), were: PFG = 0; 0 < PFG < 0.33; 0.33 ≤ PFG < 0.67; 0.67 ≤ PFG < 1 and PFG = 1. We considered each FG as the focal FG at a time (2a: legumes, 2b: tall herbs, 2c: small herbs, 2d: grasses) and displayed their effects during the years 2003–2007. In 2004, only legumes were separated from non-legumes during the biomass harvest.

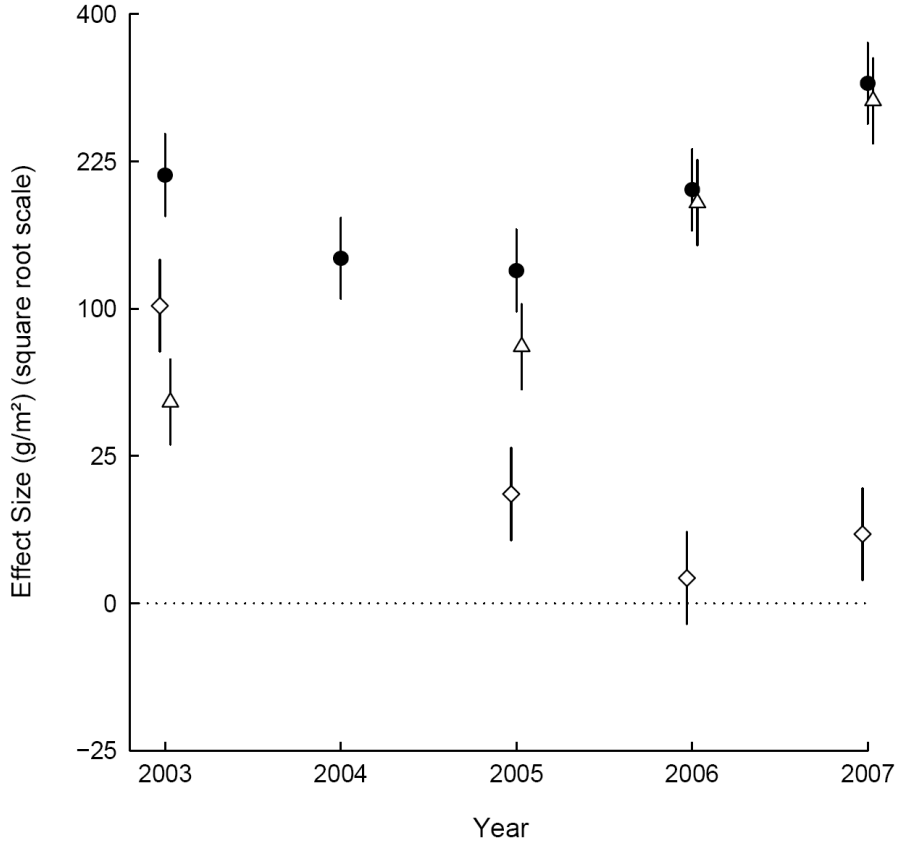

Fig. 3. Net biodiversity effect (NE, ●), complementarity effect (CE, Δ) and selection effect (SE, ◊) over time. Symbols represent means ± 1 standard error. Note the square root scale of the y-axis. For 2004, CE and SE could not be estimated because community biomass was not separated to species. Symbols were slightly jittered to improve visualization.

Appendix

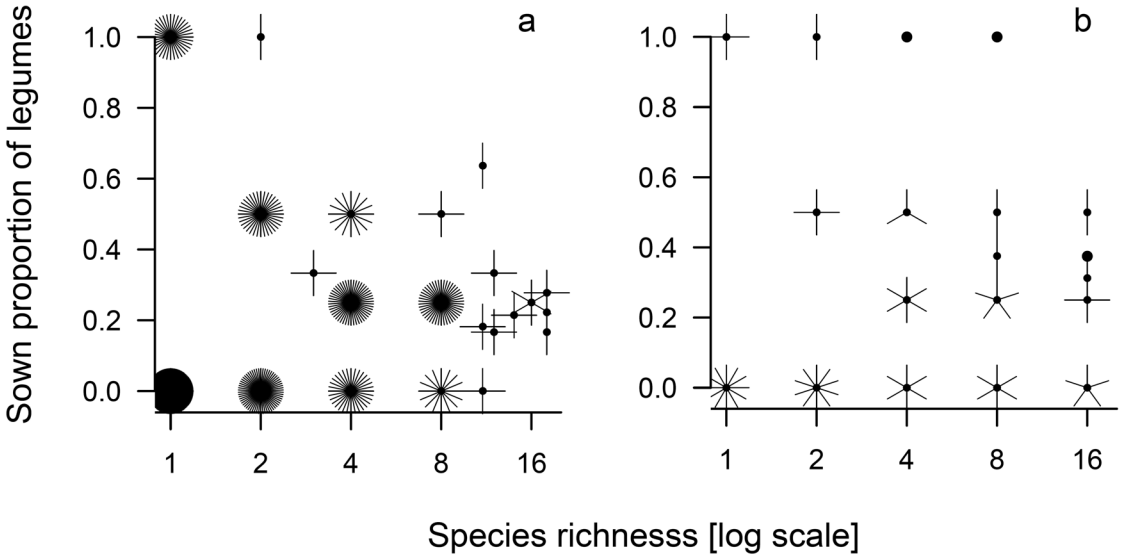

Fig. A1. Differences between (a) the design of previous biodiversity experiments, exemplified by the European BIODEPTH Experiment (Hector *et al.* 1999, Spehn *et al.* 2005) and (b) the Jena Experiment. The range of functional group proportions (here: proportions of legumes) diminishes with increasing species richness in (a) but remains large in (b). This allowed us to test effects of functional group proportions across the entire richness gradient in the present study. The number of "leaves" around the center of the flower symbols represent the number of plots (in total 476 in BIODEPTH and 78 in the Jena Experiment (a point without leaves symbolizes a single plot). Note that also for the other three functional groups (grasses, small herbs and tall herbs) the range of functional group proportions remains high across the entire richness gradient in the Jena Experiment (see also Table 1).

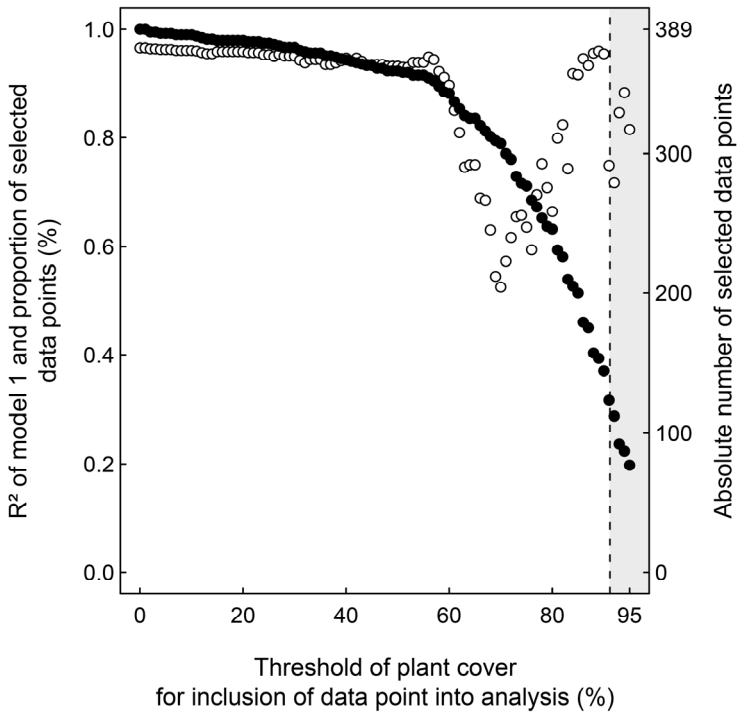

Fig. B1. Effect of selecting a sub-sample of data points on the strength of the relationship between the logarithm of species richness and aboveground community biomass. Data points were selected if derived from plots on which the vegetation cover of the target community exceeded a specified threshold. Filled symbols represent the number of selected data points (on the left axis in relative and on the right axis in absolute terms). Open symbols represent R^2 of the relationship between the logarithm of species richness and aboveground community biomass. This relationship was not significant if R^2 fell within the shaded region ($P > 0.05$). The significance of this relationship was tested by fitting model 1 to the respective subset of the data.

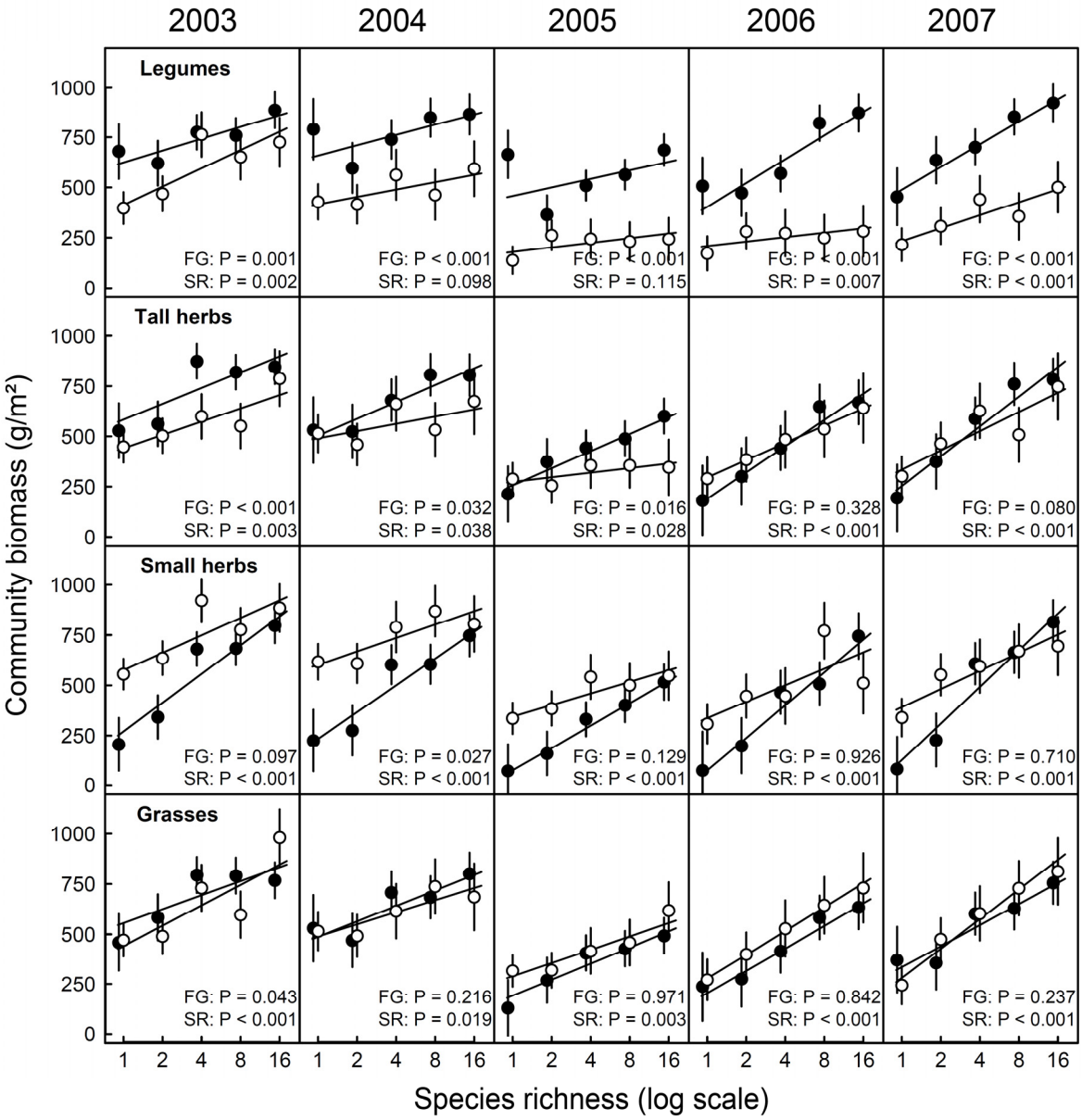

Fig. C1. Effects of presence (●) and absence (o) of the FGs legumes (first row), tall herbs (second row), small herbs (third row) and grasses (last row) on aboveground community biomass over the species richness gradient from 2003–2007. Symbols represent means ± 1 standard error. Significances, fitted lines and standard errors for the effect of the presence of the focal FG and the logarithm of species richness fitted after the focal FG were obtained from different ANOVAs for each of the 20 panels. These ANOVAs included the terms presence of the focal FG, logarithm of species richness and the interaction between these two variables. The resulting P-values of the main effects are given in the corresponding panels (FG for presence of focal group, SR for species richness), their interaction was never significant. Symbols were slightly jittered to improve visualization.

Tables D1–D3. Summary of the ANOVA for NE (D1) from 2003–2007, and CE (D2) and SE (D3) in 2003, 2005–2007 (model 1 in "Methods"), using type-I sums of squares. Indented terms show the linear contrast for FG richness and its deviation from linearity (FG composition residuals). The sum of these two terms corresponds to FG composition. Year was fitted as a 5-level factor for NE and as a 4-level factor for CE and SE. The column % contains the proportions of explained between-plot-variation.

Table D1

Source	Df	SS	MS	%	F	P
Overall mean	**1**	**58552**	**58552**	**100**	**1103.07**	**<0.001**
Between plots						
Block	3	1171	390	6	2.82	0.054
Log (species richness (SR))	**1**	**4617**	**4617**	**23**	**33.34**	**<0.001**
Functional group (FG) composition	**12**	**8846**	**737**	**44**	**5.32**	**<0.001**
FG richness	**1**	**1744**	**1744**	**9**	**12.59**	**0.001**
FG composition residuals	**11**	**7102**	**646**	**35**	**4.66**	**<0.001**
Log (SR) x FG composition	12	1099	92	5	0.66	0.774
Plot residuals	*33*	*4571*	*139*	*23*		
Within plots						
Year	**4**	**1633**	**408**		**7.69**	**<0.001**
Log (SR) x Year	4	106	27		0.50	0.736
FG composition x Year	48	2278	48		0.89	0.665
FG richness x Year	4	4	1		0.02	0.999
FG composition residuals x Year	44	2275	52		0.97	0.526
Log (SR) x FG composition x Year	48	2224	46		0.87	0.703
Residuals	*139*	*7378*	*53*			

Table D2

Source	Df	SS	MS	%	F	P
Overall mean	**1**	**32696**	**32696**	**100**	**408.20**	**<0.001**
Between plots						
Block	3	456	152	3	1.28	0.298
Log (species richness (SR))	**1**	**3061**	**3061**	**21**	**25.77**	**<0.001**
Functional group (FG) composition	**12**	**5799**	**483**	**39**	**4.07**	**0.001**
FG richness	**1**	**2111**	**2111**	**14**	**17.77**	**<0.001**
FG composition residuals	**11**	**3688**	**335**	**25**	**2.82**	**0.010**
Log (SR) x FG composition	12	1534	128	10	1.08	0.410
Plot residuals	*33*	*3921*	*119*	*27*		
Within plots						
Year	**3**	**3954**	**1318**		**16.46**	**<0.001**
Log (SR) x Year	3	109	36		0.45	0.716
FG composition x Year	36	2904	81		1.01	0.472
FG richness x Year	3	138	46		0.57	0.633
FG composition residuals x Year	33	2766	84		1.05	0.418
Log (SR) x FG composition x Year	36	2043	57		0.71	0.880
Residuals	*103*	*8250*	*80*			

Table D3

Source	Df	SS	MS	%	F	P
Overall mean	**1**	**4335**	**4335**	**100**	**35.49**	**<0.001**
Between plots						
Block	3	187	62	2	0.27	0.849
Log (species richness (SR))	1	213	213	2	0.91	0.347
Functional group (FG) composition	12	2995	250	25	1.06	0.419
FG richness	1	0	0	0	0.00	0.977
FG composition residuals	11	2995	272	25	1.16	0.350
Log (SR) x FG composition	12	944	79	8	0.34	0.976
Plot residuals	*33*	*7737*	*235*	*64*		
Within plots						
Year	**3**	**2868**	**956**		**7.82**	**<0.001**
Log (SR) x Year	3	368	123		1.00	0.394
FG composition x Year	36	6503	181		1.48	0.066
FG richness x Year	3	227	76		0.62	0.603
FG composition residuals x Year	**33**	**6276**	**190**		**1.56**	**0.048**
Log (SR) x FG composition x Year	36	6112	170		1.39	0.102
Residuals	*103*	*12582*	*122*			

Tables E1–E3. Summary of the ANOVA for NE (E1) from 2003–2007, and CE (E2) and SE (E3) in 2003, 2005–2007 (model 2 in "Methods"), using type-I sums of squares. Indented terms show two different sets of orthogonal contrasts for FG composition: (i) linear contrast for FG richness and its deviation from linearity and (ii) contrast for the presence of particular FGs and their interactions. In both cases the sum of contrast terms corresponds to FG composition. For the within plots analysis, the 2- and 3-way interactions of FGs were aggregated into the term residual FG composition. Year was fitted as a 5-level factor for NE and as a 4-level factor for CE and SE. The column % contains the proportions of explained between-plot-variation.

Table E1

Source	Df	SS	MS	%	F	P
Between plots						
Block	3	1171	390	6	2.82	0.054
Functional group (FG) composition	**12**	**11586**	**966**	**57**	**6.97**	**<0.001**
FG richness	**1**	**4144**	**4144**	**20**	**29.92**	**<0.001**
FG composition residuals	**11**	**7443**	**677**	**37**	**4.89**	**<0.001**
Main effects of presence of particular FGs	**4**	**10435**	**2609**	**51**	**18.84**	**<0.001**
Presence legumes	**1**	**9042**	**9042**	**45**	**65.28**	**<0.001**
Presence tall herbs	**1**	**1053**	**1053**	**5**	**7.60**	**0.009**
Presence small herbs	1	225	225	1	1.62	0.212
Presence grasses	1	115	115	1	0.83	0.369
2-way interactions between FGs	6	1075	179	5	1.29	0.287
Presence legumes x presence tall herbs	1	21.6	21.6	0	0.16	0.695
Presence legumes x presence small herbs	1	5.5	5.5	0	0.04	0.843
Presence legumes x presence grasses	1	188.2	188.2	1	1.36	0.252
Presence tall herbs x presence small herbs	1	166.8	166.8	1	1.20	0.280
Presence tall herbs x presence grasses	1	72.4	72.4	0	0.52	0.475
Presence small herbs x presence grasses	**1**	**620.3**	**620.3**	**3**	**4.48**	**0.042**
3-way interactions between FGs**	2	77	38	0	0.28	0.759
Log (species richness (SR))	**1**	**1877**	**1877**	**9**	**13.55**	**0.001**
FG composition x log (SR)	12	1099	92	5	0.66	0.774
Plot residuals	*33*	*4571*	*139*	*23*		
Within plots						
Year	**4**	**1633**	**408**		**7.69**	**<0.001**
FG composition x Year	48	2318	48		0.91	0.640
FG richness x Year	4	13	3		0.06	0.993
FG composition residuals x Year	44	2304	52		0.99	0.505
Presence of particular FGs x Year	16	1297	81		1.53	0.099
Presence legumes x Year	4	399	100		1.88	0.118
Presence tall herbs x Year	**4**	**623**	**156**		**2.93**	**0.023**
Presence small herbs x Year	4	186	46		0.87	0.481

Presence grasses x Year	4	90	22	0.42	0.793
Residual FG composition x Year	32	1021	32	0.60	0.953
Log (SR) x Year	4	67	17	0.32	0.867
Presence legumes x log (SR) x Year	**4**	**804**	**201**	**3.79**	**0.006**
Residual log (SR) x Year	44	1420	32	0.61	0.971
Residuals	*139*	*7378*	*53*		

Table E2

Source	Df	SS	MS	%	F	P
Between plots						
Block	3	456	152	3	1.28	0.298
Functional group (FG) composition	**12**	**7879**	**657**	**53**	**5.53**	**<0.001**
FG richness	**1**	**4027**	**4027**	**27**	**33.90**	**<0.001**
FG composition residuals	**11**	**3852**	**350**	**26**	**2.95**	**0.008**
Main effects of presence of particular FGs	**4**	**6432**	**1608**	**44**	**13.54**	**<0.001**
Presence legumes	**1**	**5479**	**5479**	**37**	**46.12**	**<0.001**
Presence tall herbs	**1**	**737**	**737**	**5**	**6.20**	**0.018**
Presence small herbs	1	48	48	0	0.40	0.529
Presence grasses	1	168	168	1	1.41	0.243
2-way interactions between FGs	6	1306	218	9	1.83	0.123
Presence legumes x tall herbs	1	1	1	0	0.01	0.935
Presence legumes x small herbs	1	31	31	0	0.26	0.612
Presence legumes x grasses	1	137	137	1	1.15	0.291
Presence tall herbs x small herbs	**1**	**734**	**734**	**5**	**6.17**	**0.018**
Residual 2-way interactions between FGs*	2	404	202	3	1.70	0.198
3-way interactions between FGs**	2	141	70	1	0.59	0.558
Log (species richness (SR))	**1**	**981**	**981**	**7**	**8.26**	**0.007**
FG composition x log (SR)	12	1534	128	10	1.08	0.410
Plot residuals	*33*	*3921*	*119*	*27*		
Within plots						
Year	**3**	**3954**	**1318**		**16.46**	**<0.001**
FG composition x Year	36	2998	83		1.04	0.426
FG richness x Year	3	193	64		0.80	0.495
FG composition residuals x Year	33	2805	85		1.06	0.398
Presence of particular FGs x Year	12	1359	113		1.41	0.172
Presence legumes x Year	3	352	117		1.46	0.229
Presence tall herbs x Year	3	8	3		0.03	0.992
Presence small herbs x Year	3	361	120		1.50	0.218
Presence grasses x Year	3	638	213		2.66	0.052
Residual FG composition x Year	24	1640	68		0.85	0.663
Log (SR) x Year	3	14	5		0.06	0.981
FG composition x log (SR) x Year	36	2043	57		0.71	0.880
Residuals	*103*	*8250*	*80*			

Table E3

Source	Df	SS	MS	%	F	P
Between plots						
Block	3	187	62	2	0.27	0.849
Functional group (FG) composition	12	3059	255	25	1.09	0.402
FG richness	1	35	35	0	0.15	0.703
FG composition residuals	11	3025	275	25	1.17	0.342
Main effects of presence of particular FGs	4	1228	307	10	1.31	0.287
Presence legumes	1	887	887	7	3.78	0.060
Presence tall herbs	1	8	8	0	0.03	0.859
Presence small herbs	1	275	275	2	1.17	0.286
Presence grasses	1	58	58	0	0.25	0.622
2-way interactions between FGs	6	1449	242	12	1.03	0.424
Presence legumes x tall herbs	1	30	30	0	0.13	0.722
Presence legumes x small herbs	1	3	3	0	0.01	0.908
Presence legumes x grasses	1	67	67	1	0.29	0.597
Presence tall herbs x small herbs	**1**	**1274**	**1274**	**11**	**5.43**	**0.026**
Residual 2-way interactions between FGs*	2	75	38	1	0.16	0.852
3-way interactions between FGs**	2	382	191	3	0.82	0.451
Log (species richness (SR))	1	149	149	1	0.63	0.431
FG composition x log (SR)	12	944	79	8	0.34	0.976
Plot residuals	*33*	*7737*	*235*	*64*		
Within plots						
Year	**3**	**2868**	**956**		**7.82**	**<0.001**
FG composition x Year	**36**	**6778**	**188**		**1.54**	**0.048**
FG richness x Year	3	389	130		1.06	0.369
FG composition residuals x Year	**33**	**6389**	**194**		**1.58**	**0.042**
Presence of particular FGs x Year	12	2447	204		1.67	0.085
Presence legumes x Year	3	63	21		0.17	0.915
Presence tall herbs x Year	**3**	**1089**	**363**		**2.97**	**0.035**
Presence small herbs x Year	3	442	148		1.21	0.311
Presence grasses x Year	3	853	284		2.33	0.079
Residual FG composition x Year	24	4331	180		1.48	0.093
Log (SR) x Year	3	93	31		0.25	0.858
FG composition x log (SR) x Year	36	6112	170		1.39	0.102
Residuals	*103*	*12582*	*122*			

** includes presence tall herbs x grasses, presence small herbs x grasses; ** includes presence legumes x tall herbs x small herbs and presence legumes x tall herbs x grasses*

Chapter 2

Contrasting species performance in monoculture and mixture explains temporal changes in biodiversity effects

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Abstract

Numerous studies have reported positive but temporally variable effects of species richness on the productivity of plant communities. Such biodiversity effects are usually quantified by comparing the performance of species in mixture with their performance in monoculture. Therefore, increasing biodiversity effects either result from a positive development of mixtures or from a negative development of monocultures. While positive trends in the performance of mixtures may indicate increasing resource complementarity or facilitation, negative trends in the performance of monocultures suggest either a lack of these mechanisms or other phenomena, such as the accumulation of pathogens or toxic compounds or the imbalanced depletion of resources over time. Here, we analyzed the temporal dynamics of monoculture and mixture yields over a 5-year period in a large-scale biodiversity experiment (Jena Experiment). We found strong evidence for differences in the temporal dynamics of species performances between monocultures and mixtures. In monocultures, species were more likely to have declining productivities over time than in mixtures, especially during the early years of the experiment. However, the average performance of monocultures was stable during the later years of the experiment and negative trends in the development of monocultures did not solely explain why the mean net biodiversity effect increased during that time period. Instead, a promotion of the growth of species in mixtures was the predominant cause of the increasing net biodiversity effects, indicating beneficial or facilitative interactions among different species. Individual species performances were highly variable over time and mean changes in the net biodiversity effect were strongly impacted by changes in the productivity of particular species.

Introduction

Results of numerous biodiversity experiments suggest that plant communities are more productive and more efficient in nutrient cycling when they contain higher numbers of species (Hooper *et al.* 2005; Spehn *et al.* 2005; Balvanera *et al.* 2006). A common measure to quantify such positive biodiversity effects at the community level is the net biodiversity effect (net effect). If aboveground biomass production is the relevant ecosystem function, the net effect of a community equals the absolute difference between its aboveground biomass (observed yield) and a theoretically expected value derived from the performance of the composing species in monoculture (expected yield). Thus, temporal changes in net effects reflect diverging trends in species performance between monoculture and mixture.

In experiments that manipulated plant species richness the average net effect on aboveground biomass production often increased over time (e.g. Spehn *et al.* 2005; Van Ruijven & Berendse 2005; Tilman *et al.* 2006a; Fargione *et al.* 2007); (see also meta-analysis of Cardinale *et al.* 2007) or at least during several consecutive years (Marquard *et al.* 2009; Van Ruijven & Berendse 2009). Such positive trends in net effects over time have been explained by increasing effects of resource complementarity, leading to improved acquisition and retention of limiting resources in diverse communities (Pacala & Tilman 2002; Spehn *et al.* 2005; Fargione *et al.* 2007). This implies that net effects tend to increase because mixtures gradually improve their performance. However, it is similarly plausible that net effects increase because monocultures gradually decrease in performance, for example due to negative plant–soil feedbacks (Bonanomi *et al.* 2005a; Casper & Castelli 2007; Petermann *et al.* 2008; Van der Heijden *et al.* 2008). Plants may change the soil in which they grow for the worse by an imbalanced depletion of resources (Schenk 2006), the release of toxic compounds (Singh *et al.* 1999) or the accumulation of pathogens over time (Van der Putten *et al.* 1993; Petermann *et al.* 2008). Furthermore, species may be attacked more severely by host-specific foliar pathogens in monoculture than in mixture if these pathogens respond positively to increasing host frequency (Mitchell *et al.* 2003; Hille Ris Lambers *et al.* 2004). Indeed, long-standing agricultural knowledge suggests that a single plant species is likely to decline in its yield if grown in monoculture at the same site for multiple years. However, monoculture performance over time has hardly ever been studied in the context of diversity–ecosystem functioning relationships. Some previous studies conducted in biodiversity experiments compared the performance of different species in monoculture (e.g. Hector *et al.* 2002; Heisse *et al.* 2007) or across a diversity gradient (Tilman *et al.* 1997; Troumbis *et al.* 2000; Hector *et al.* 2002; Van Ruijven & Berendse 2003; Dimitrakopoulos & Schmid 2004;

Hille Ris Lambers *et al.* 2004; Roscher *et al.* 2007) but only at a single point in time. Where biodiversity experiments were used to compare the performance of species over multiple years the focus was often on the temporal stability of biomass production (Van Ruijven & Berendse 2007; Isbell *et al.* 2009). So far, no study has explicitly addressed the question whether net effects tend to increase due to improving mixtures or degrading monocultures.

Here, we present a detailed analysis of temporal changes in net effects that occurred over a period of 5-years in a large-scale biodiversity experiment (Jena Experiment). During that time period, the mean net effect (averaged across all experimental communities) was constantly positive but first decreased from 2003–2005 and then increased from 2005–2007 (Marquard *et al.* 2009). We assessed whether these changes in the mean net effect resulted predominantly from changes in the performance of the reference monocultures or from changes in the performance of the species in mixtures. Specifically, we asked: (1) does the temporal development of productivity differ between monocultures and mixtures? (2) Was the increase in the mean net effect observed in the Jena Experiment from 2005–2007 mainly due to a negative development of the performance of species in monoculture? (3) Did the majority of species in the Jena Experiment change their performance in accordance with changes in the mean net effect?

Methods

FIELD SITE AND BIOMASS SAMPLING

The Jena Experiment is a biodiversity experiment near Jena, Germany (50°55’ N, 11°35’ E, 130 m NN). In 2002, 198 plant communities were sown containing various combinations of 1, 2, 4, 8, or 16 herbaceous grassland species. Plot size was either 3.5 x 3.5 m (120 small monocultures) or 20 x 20 m (16 large monocultures and 62 mixtures with 2–16 species). Species composition of each plot was determined by a random draw from a pool of 60 species. Plots were not fertilized or irrigated but mown and weeded twice a year. The field site was divided into four blocks, each containing four large plots of the species richness levels 1, 2, 4 and 8, three or four 16-species mixtures and 30 monocultures of small plot size. For more details about the design, establishment and maintenance of the Jena Experiment, see Roscher *et al.* (2004).

From 2003–2007, aboveground plant biomass was harvested twice a year (during peak standing biomass in late May and in late August) by clipping the vegetation at 3 cm above ground in four (in May 2005 and August 2007 only three) randomly placed sampling frames of 0.2 x 0.5 m per large plot and in two randomly placed sampling frames of 0.2 x 0.5 m per

small monoculture. The harvested biomass was sorted into target species and dried at 70 °C for at least 48 h. In August 2004, the harvested target species were sorted into legumes and non-legumes only. More detailed information about the sampling regime is given in Marquard *et al.* (2009).

DATA ANALYSIS

Aboveground biomass at the time of the harvests was calculated for each experimental community as the mean of the sampling frames per plot. Annual aboveground community biomass (hereafter community biomass) was calculated as the sum of the two harvests per year. We determined the net effect for every community using the additive partitioning method of Loreau & Hector (2001, for more details see Marquard *et al.* 2009) and averaged these values per species richness level. To analyze how changes in species abundances affected changes in the net effect we plotted changes in the expected yield of a species against changes in the observed yield of a species for each species richness level (Fig. 2). Changes in the expected yield of a species (ΔY_{Ei}) were calculated as follows:

$$\Delta Y_{Ei} = 1/SR * (Ymono_i \text{ in year } (x + 2) - Ymono_i \text{ in year } (x)),$$

where $Ymono_i$ = the average of the annual biomass of the two small monocultures of species i in g/m^2 and SR = species richness level for which the changes in expected yield are calculated. Changes in the observed yield of a species (ΔY_{Oi}) were calculated as follows:

$$\Delta Y_{Oi} = 1/N_i * \sum (Ymix_{i\,j} \text{ in year } (x + 2) - Ymix_{i\,j} \text{ in year } (x)),$$

where $Ymix_{i\,j}$ = the annual biomass of species i in g/m^2 in the particular community j and N_i = number of plots on which species i was present. Note that all temporal changes were calculated for 2-year periods (2003–2005 and 2005–2007). We chose these time intervals because no species-specific biomass data was available for 2004. However, 2-year time steps corresponded well to the temporal dynamics in aboveground productivity observed in the Jena Experiment (a period of decline and a period of growth, see "Results"). To improve the normality of the error distribution, the absolute values for the changes in the expected yield and the observed yield of a species were square-root transformed and the result was multiplied by –1 if the original value was negative. Considering the four quadrants of the coordinate systems in Fig. 2 helped to distinguish the following four cases: over time, a species could (i) increase in monoculture and in mixture (first quadrant), (ii) decrease in monoculture but increases in mixture (second quadrant), (iii) decrease in monoculture as well as in mixture (third quadrant), and (iv) increase in monoculture but decrease in mixture (fourth quadrant). If a species changed its performance in mixture by the amount predicted

from its performance in monoculture (i.e., a shift in the expected yield equaled a shift in the observed yield), its position in the diagram would fall on the diagonal that crosses the first and third quadrant (broken line in Fig. 2). A point falling below this diagonal contributed to a decline in the net effect, whereas a point falling above this diagonal contributed to an increase in the net effect.

For an alternative analysis of temporal trends in the performance of species in monoculture and mixture, we calculated the annual relative growth rate for each species in each experimental community (RGR_i) as follows:

$RGR_{i\ \text{year x–year (x + 1)}} = \ln(Y_{i\,j}\ \text{in year (x + 1)}) - \ln(Y_{i\,j}\ \text{in year (x)})$,

where $Y_{i\,j}$ = the annual biomass of species i in g/m^2 in the particular community j. Here, the annual biomass of the two replicate monocultures was not averaged but RGR_i was calculated for every monoculture plot separately. Due to the lack of $Y_{i\,j}$-data for mixtures in 2004 we could not calculate $RGR_{i\ 2003\text{-}2004}$ and $RGR_{i\ 2004\text{-}2005}$ for species in mixtures. Given the obvious bimodal pattern in the temporal development of aboveground productivity (see above and "Results"), we overcame this drawback by calculating mean RGR_i-values ($MRGR_i$) for time intervals of two years as follows

for monocultures: $MRGR_{i\ 2003\text{-}2005} = (RGR_{i\ 2003\text{-}2004} + RGR_{i\ 2004\text{-}2005})/2$,

$MRGR_{i\ 2005\text{-}2007} = (RGR_{i\ 2005\text{-}2006} + RGR_{i\ 2006\text{-}2007})/2$;

and for mixtures: $MRGR_{i\ 2003\text{-}2005} = (\ln(Y_{i\,j}\ \text{in year 2005}) - \ln(Y_{i\,j}\ \text{in year 2003}))/2$,

$MRGR_{i\ 2005\text{-}2007} = (RGR_{i\ 2005\text{-}2006} + RGR_{i\ 2006\text{-}2007})/2$.

To assess whether $MRGR_i$ differed between monocultures and mixtures and how it was affected by plot size, species richness and functional group identity, we fitted a linear mixed effects model to the two $MRGR_i$ data sets (for the time intervals 2003–2005 and 2005–2007, Tables 1a,b), using restricted maximum likelihood (REML). The contrast between monocultures and mixtures (M), plot size, $\log_2$(species richness), species richness (deviation from log-linearity) and functional group identity as well as the 2-way interactions between the first four terms and functional group identity were fitted as fixed effects (fixed model: constant + M + plot size + $\log_2$(species richness) + species richness (as factor) + functional group (FG) identity + M x FG identity + plot size x FG identity + $\log_2$(species richness) x FG identity + species richness (as factor) x FG identity). Block, plot and species identity were fitted as random effects (random model: block + plot + species identity + plot x species identity), whereby the interaction between plot and species identity represented the residual variance. A weighting variable accounted for the differences in the calculations of the $MRGR_i$ data between monocultures and mixtures (see above). It would have been desirable to

integrate "time" as an explanatory variable into the model and to fit it to a data set including $MRGR_i$ data for the time intervals 2003–2005 and 2005–2007. However, we could not compute this analysis due to the complexity of interactions between species identity, plot and time.

In addition, we averaged the $MRGR_i$ values for the time intervals 2003–2005 and 2005–2007 across plots (i) for all species, (ii) for species belonging to a particular functional group and (iii) for the species individually. We tested whether the overall means (i) and the means per functional group (ii) differed significantly from zero by ANOVA and display the mean values per species (iii) as well as the mean values per functional group (ii) in Table 2.

We ran the REML in GenStat (11th edition, VSN International), and used the statistical software R (Version 2.7.2; http://www.r-project.org) for all other calculations and analyses.

Results

Positive effects of species richness on aboveground community biomass and on the net effect were previously described for the Jena Experiment (see Roscher *et al.* 2005 for an analysis of the May harvest in 2003; and Marquard *et al.* 2009 for an analysis of annual biomass from 2003–2007). Figure 1 illustrates these positive effects of species richness on both measures and shows that they were consistent through the years.

Regarding temporal changes in aboveground community biomass and the net effect, two phases were distinguishable: from 2003–2005, both measures declined and from 2005–2007, both measures increased again (Fig. 1a and 1b). While the decline in aboveground productivity during the first three years of the experiment was similar in monocultures and mixtures, the increase in aboveground productivity during the later years was strong in mixtures but nearly absent in monocultures (Fig. 1a). This average performance of all species therefore shows that the increase in the net effect during 2005–2007 resulted from an enhancement of the mean productivity in mixtures rather than from a further decline of the mean productivity in monocultures.

The magnitude of absolute changes in expected yield and observed yield varied greatly among species richness levels and among species (Fig. 2). The variation in absolute changes in expected yield as well as in observed yield declined as the average proportional abundance of the species decreased with increasing species richness. Temporal changes in the net effect increased with increasing species richness (dNE values in lower right corner of panels in Fig. 2, exception: from 2003–2005, net effects changed on average slightly more in 4-species than in 8-species mixtures).

From 2003–2005, the majority of species shifted to a lower productivity in monoculture as well as in mixture (many data points in the third quadrant; Fig. 2, left column). While only few species increased productivity in monoculture from 2003–2005 (few points in the first or forth quadrant), the proportion of species that increased productivity in mixture and decreased it in monoculture was much higher and increased with species richness (increasing number of points in second quadrant with increasing species richness). Points below the diagonal fell mostly in the third quadrant. Thus, species contributing to the negative trend in the net effect were mostly those that produced less biomass in mixture as well as in monoculture, whereby the negative development of these species was stronger in mixtures than in monoculture.

From 2005–2007, approximately half of the species shifted to a lower productivity and the other half to a higher productivity in monoculture (approximately same number of data points in the first and fourth quadrant as in the second and third quadrant; Fig. 2, right column). The majority of species increased their productivity in mixture (points in the first and second quadrant) but a number of species showed the opposite trend and decreased their productivity in mixture, in particular at high species richness (points in the third and fourth quadrant). Whereas during the early years of the experiment species rarely declined in mixture if they increased there performance in monoculture, such opposite temporal trends were rather common during the later years (points in the fourth quadrant). Points above the diagonal fell mostly in the first and second quadrant. Thus, species contributing to the positive trend in the net effect were mostly those which became more abundant in mixture. Their development in monoculture ranged from positive to negative.

During both phases, $MRGR_i$ differed significantly between monocultures and mixtures ("Contrast between monocultures and mixtures (M)" in Tables 1a,b). This difference increased from the first to the second phase (larger F-value during the second than during the first phase, Tables 1a,b). Neither plot size nor species richness or functional group identity affected $MRGR_i$ during any of the time periods. However, there was always large variation in $MRGR_i$ among species (see large variance component for the random term "species identity" in Tables 1a,b).

Averaged across all plots and species, $MRGR_i$ was negative for species growing in mixtures (-0.25 ± 0.06; $P < 0.001$) as well as for species growing in monocultures (-0.36 ± 0.06; $P < 0.001$) during the first phase of the experiment (2003–2005). During the second phase of the experiment (2005–2007), the average $MRGR_i$ was positive for species growing

in mixtures (0.41 ± 0.07; $P < 0.001$) and not significantly different from zero for species growing in monocultures (0.05 ± 0.05; $P = 0.403$).

Table 2 shows the average $MRGR_i$ for each species and for the four functional groups growing in mixture or monoculture. Regarding the functional groups, only grasses had a significantly negative average $MRGR_i$ in mixture during the first phase. In monoculture, only legumes showed on average no significant decline. During the second phase, the average performance of all four functional groups increased significantly in mixture and remained constant in monoculture.

Discussion

In the Jena Experiment, biomass production was highly dynamic over time. Fluctuations in aboveground biomass production have been reported from other grassland biodiversity experiments (Pfisterer *et al.* 2004; Tilman *et al.* 2006b; Lanta & Lepš 2007; Van Ruijven & Berendse 2009) and may be caused by variable climatic conditions or changes in the availability of resources. When the Jena Experiment was set up, the topsoil was loosened by harrowing and this could have made additional nutrients available. The decline in aboveground biomass production and in the mean net effects per species richness level that occurred during the first three years of the Jena Experiment (2003–2005) may have been related to this initial "fertilizing effect" fading away. Interestingly, aboveground biomass production and mean net effects increased again during the later years of the experiment (2005–2007). This bimodal pattern in the temporal development of biomass and net effects allowed us to contrast the performance of species in monoculture and mixture during a period of descent as well as during a period of increasing biomass production.

Our results demonstrated that the temporal development of biomass production differed between monocultures and mixtures in both phases. Species in mixtures generally performed better, as shown by their, on average, larger annual relative growth rate. However, the direction of change was the same during the first phase (negative in monocultures and in mixtures) and different only during second phase (positive in mixtures vs. neutral in monocultures). This indicated that the force affecting adversely the productivity in monocultures and mixtures during the first phase (possibly a decline in available nutrients) was stronger than potential mechanisms that could cause monocultures and mixtures to diverge. Those became more effective during the later years, which is consistent with previous studies reporting an increasing net effect over time time (e.g. Spehn *et al.* 2005, Van Ruijven & Berendse 2005, Tilman *et al.* 2006, Fargione *et al.* 2007). We could demonstrate

that species in monocultures and mixtures differed with regard to the development of their productivity over time, independently of plot size and functional group identity (see Tables 1a,b). However, comparing the average annual growth rate per functional group separately showed that the on average negative trend of species in mixture during the first phase was mainly the result of a declining productivity of grasses. Possibly, grasses profited more from the "fertilizing effect" caused by the initial soil treatment than did the remaining functional groups.

Contrasting temporal dynamics in observed and expected yields showed that species with a more negative trend in mixture than in monoculture were mainly responsible for the decrease in the mean net effect, whereas its increase was predominantly caused by species with a positive trend in mixture and a less positive or even negative trend in monoculture. This indicated that changes in the performance of species in mixtures were largely responsible for the variation in the mean net effect over time. The minor contribution of species with a negative trend in monoculture and a neutral or less negative trend in mixture (few points in the third quadrant above the diagonal in Fig. 2, right column) to the increase in the mean net effect contradicted the hypothesis that increasing net effects were predominantly the result of a decline in monoculture productivity over time. We conclude that degrading monocultures were a common phenomenon in our experiment but not the predominant cause for increasing net effects. Thus, negative plant–soil feedbacks or increased attack of foliar pathogens may have played a role in generating positive biodiversity effects (Petermann *et al.* 2009) but other mechanisms such as resource complementarity and facilitation were probably of greater importance. Negative plant–soil feedbacks have been demonstrated recently in field trials (Bonanomi *et al.* 2005b; Bell *et al.* 2006; Casper & Castelli 2007), and a decrease in plant diversity has been reported to increase the load of foliar pathogens (Knops *et al.* 1999; Mitchell *et al.* 2003). However, whether negative effects of pathogens on plant species indeed increase with host frequency (i.e., with a decrease in diversity) and the role of host abundance (in term of biomass) is still under debate (Knops *et al.* 1999; Klironomos 2002; Mitchell *et al.* 2003; Hille Ris Lambers *et al.* 2004; Bell *et al.* 2006 for contrasting results and Hille Ris Lambers *et al.* 2004; Van der Heijden *et al.* 2008 for a discussion thereof).

In our study, temporal trends in the biomass production of individual species were highly variable in monocultures as well as in mixtures (see Fig. 2). Considerable variation among the temporal trends in species productivity were previously observed in studies comparing the performance of species in 8-species mixtures (Van Ruijven & Berendse 2007) or 16-species mixtures (Hille Ris Lambers *et al.* 2004) over multiples years. Our analyses of

observed and expected yields showed that comparatively few species were responsible for the negative trend in the mean net effect during the first phase, while numerous species with degrading monocultures improved their performance in mixtures and thereby counteracted the decrease in the mean net effect. Similarly, numerous species prevented an even stronger positive trend in the mean net effect during the second phase, by a relatively better performance in monoculture than in mixture. We conclude that the mean changes in the net effect were not reflecting temporal changes in species abundance shared by the majority of species. Instead, the mean changes in the net effects were strongly impacted by temporal trends in particular species. We would like to point out that this conclusion is not in contradiction to a decrease in the mean selection effect over time reported by Marquard *et al.* (2009) for the same experiment. Selection effects measure the covariance between the performance of a species in monoculture and mixture (Loreau & Hector 2001). Thus, a decrease in the selection effect may indicate that the relationship between monoculture and mixture yield weakens which is fully compatible with our observation of strong effects of single species on temporal changes in the mean net effect.

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Chapter references

Balvanera P., Pfisterer A. B., Buchmann N., He J.-S., Nakashizuka T., Raffaelli D. & Schmid B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, **9**, 1-11.

Bell T., Freckleton R. P. & Lewis O. T. (2006). Plant pathogens drive density-dependent seedling mortality in a tropical tree. *Ecology Letters*, **9**, 569-574.

Bonanomi G., Giannino F. & Mazzoleni S. (2005a). Negative plant-soil feedback and species coexistence. *Oikos*, **111**, 311-321.

Bonanomi G., Rietkerk M., Dekker S. C. & Mazzoleni S. (2005b). Negative plant-soil feedback and positive species interaction in a herbaceous plant community. *Plant Ecology*, **181**, 269-278.

Cardinale B. J., Wrigh J. P., Cadotte M. W., Carroll I. T., Hector A., Srivastava D. S., Loreau M. & Weis J. J. (2007). Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences*, **104**, 18123-18128.

Casper B. B. & Castelli J. P. (2007). Evaluating plant-soil feedback together with competition in a serpentine grassland. *Ecology Letters*, **10**, 394-400.

Dimitrakopoulos P. G. & Schmid B. (2004). Biodiversity effects increase linearly with biotope space. *Ecology Letters*, **7**, 574-583.

Fargione J., Tilman D., Dybzinski R., Hille Ris Lambers J., Clark C., Harpole W. S., Knops J. M. H., Reich P. B. & Loreau M. (2007). From selection to complementarity: shifts in the causes of biodiversity-productivity relationships in a long-term biodiversity experiment. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **274**, 871-876.

Hector A., Bazeley-White E., Loreau M., Otway S. & Schmid B. (2002). Overyielding in grassland communities: testing the sampling effect hypothesis with replicated biodiversity experiments. *Ecology Letters*, **5**, 502-511.

Heisse K., Roscher C., Schumacher J. & Schulze E. D. (2007). Establishment of grassland species in monocultures: different strategies lead to success. *Oecologia*, **152**, 435-447.

Hille Ris Lambers J., Harpole S. W., Tilman D., Knops J. & Reich P. B. (2004). Mechanisms responsible for the positive diversity-productivity relationship in Minnesota grasslands. *Ecology Letters*, **7**, 661-668.

Hooper D. U., Chapin F. S., Ewel J. J., Hector A., Inchausti P., Lavorel S., Lawton J. H., Lodge D. M., Loreau M., Naeem S., Schmid B., Setälä H., Symstad A. J., Vandermeer J. & Wardle D. A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3-35.

Isbell F. I., Polley H. W. & Wilsey B. J. (2009). Biodiversity, productivity and the temporal stability of productivity: patterns and processes. *Ecology Letters*, **12**, 443-451.

Klironomos J. N. (2002). Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature*, **417**, 67-70.

Knops J. M. H., Tilman D., Haddad N. M., Naeem S., Mitchell C. E., Haarstad J., Ritchie M. E., Howe K. M., Reich P. B., Siemann E. & Groth J. (1999). Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters*, **2**, 286-293.

Lanta V. & Lepš J. (2007). Effects of species and functional group richness on production in two fertility environments: an experiment with communities of perennial plants. *Acta Oecologica*, **32**, 93-103.

Loreau M. & Hector A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, **412**, 72-76.

Marquard E., Weigelt A., Temperton V. M., Roscher C., Schumacher J., Buchmann N., Fischer M., Weisser W. W. & Schmid B. (2009). Plant species richness and functional composition drive overyielding in a 6-year grassland experiment. *Ecology*, **in press**.

Mitchell C. E., Reich P. B., Tilman D. & Groth J. V. (2003). Effects of elevated CO2, nitrogen deposition, and decreased species diversity on foliar fungal plant disease. *Global Change Biology*, **9**, 438-451.

Pacala P. & Tilman D. (2002). The transition from sampling to complementarity. In: *Functional consequences of biodiversity: Experimental progress and theoretical extensions* (eds. Kinzig A., Tilman D. & Pacala P.). Princeton University Press Princeton, New Jersey, pp. 151-166.

Petermann J. S., Fergus A. J. F., Turnbull L. A. & Schmid B. (2008). Janzen-Connell effects are widespread and strong enough to maintain diversity in grasslands. *Ecology*, **89**, 2399-2406.

Petermann J. S., Fergus A. J. F., Roscher C., Turnbull L. A., Weigelt A. & Schmid B. (2009). Biology, chance or history? The predictable re-assembly of temperate grassland communities. *Ecology*, **in press**.

Pfisterer A. B., Joshi J., Schmid B. & Fischer M. (2004). Rapid decay of diversity-productivity relationships after invasion of experimental plant communities. *Basic and Applied Ecology*, **5**, 5-14.

Roscher C., Schumacher J., Baade J., Wilcke W., Gleixner G., Weisser W. W., Schmid B. & Schulze E.-D. (2004). The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. *Basic and Applied Ecology*, **5**, 107-121.

Roscher C., Temperton V. M., Scherer-Lorenzen M., Schmitz M., Schumacher J., Schmid B., Buchmann N., Weisser W. W. & Schulze E.-D. (2005). Overyielding in experimental grassland communities - irrespective of species pool or spatial scale. *Ecology Letters*, **8**, 419-429.

Roscher C., Schumacher J., Weisser W. W., Schmid B. & Schulze E. D. (2007). Detecting the role of individual species for overyielding in experimental grassland communities composed of potentially dominant species. *Oecologia*, **154**, 535-549.

Rothmaler R. (2002). Exkursionsflora von Deutschland. Bd. 4. Kritischer Band. In: *Exkursionsflora von Deutschland* (eds. Jäger E. & Werner K.). Spektrum Heidelberg.

Schenk H. J. (2006). Root competition: beyond resource depletion. *Journal of Ecology*, **94**, 725-739.

Singh H. P., Batish D. R. & Kohli R. K. (1999). Autotoxicity: Concept, organisms, and ecological significance. *Crit. Rev. Plant Sci.*, **18**, 757-772.

Spehn E. M., Hector A., Joshi J., Scherer-Lorenzen M., Schmid B., Bazeley-White E., Beierkuhnlein C., Caldeira M. C., Diemer M., Dimitrakopoulos P. G., Finn J. A., Freitas H., Giller P. S., Good J., Harris R., Högberg P., Huss-Danell K., Jumpponen A., Koricheva J., Leadley P. W., Loreau M., Minns A., Mulder C. P. H., O'Donovan G., Otway S. J., Palmborg C., Pereira J. S., Pfisterer A. B., Prinz A., Read D. J., Schulze E.-D., Siamantziouras A.-S. D., Terry A. C., Troumbis A. Y., Woodward F. I., Yachi S. & Lawton J. H. (2005). Ecosystem effects of biodiversity manipulations in European grasslands. *Ecological Monographs*, **75**, 37-63.

Tilman D., Knops J., Wedin D., Reich P., Ritchie M. & Siemann E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, **277**, 1300-1302.

Tilman D., Hill J. & Lehman C. (2006a). Carbon-negative biofuels from low-input high-diversity grassland biomass. *Science*, **314**, 1598-1600.

Tilman D., Reich P. B. & Knops J. M. (2006b). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, **441**, 629-632.

Troumbis A. Y., Dimitrakopoulos P. G., Siamantziouras A. S. D. & Memtsas D. (2000). Hidden diversity and productivity patterns in mixed Mediterranean grasslands. *Oikos*, **90**, 549-559.

Van der Heijden M. G. A., Bardgett R. D. & Van Straalen N. M. (2008). The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters*, **11**, 296-310.

Van der Putten W. H., Van Dijk C. & Peters B. A. M. (1993). Plant-specific soil-borne diseases contribute to succession in foredune vegetation. *Nature*, **362**, 53-56.

Van Ruijven J. & Berendse F. (2003). Positive effects of plant species diversity on productivity in the absence of legumes. *Ecology Letters*, **6**, 170-175.

Van Ruijven J. & Berendse F. (2005). Diversity-productivity relationships: initial effects, long-term patterns, and underlying mechanisms. *Proceedings of the National Academy of Sciences*, **102**, 695-700.

Van Ruijven J. & Berendse F. (2007). Contrasting effects of diversity on the temporal stability of plant populations. *Oikos*, **116**, 1323-1330.

Van Ruijven J. & Berendse F. (2009). Long-term persistence of a positive plant diversity–productivity relationship in the absence of legumes. *Oikos*, **118**, 101-106.

Table 1. REML variance components analysis for annual relative growth rates per species during the time periods 2003–2005 (a) and 2005–2007 (b). For details about the calculation of these annual relative growth rates see "Methods". Abbreviations: s.e. = standard error, Wald stat. = Wald statistic, n.d.f. = numerator degrees of freedom, F = variance ratio, d.d.f. = denominator degrees of freedom, F pr = probability of obtaining F-ratio by chance. Analysis calculated with GenStat (11th edition, VSN International).

Table 1a

Variance components for random terms	Estimate	s.e.
Block	0.000	bound
Plot	0.051	0.030
Species identity	0.368	0.089
Residual = Plot x species identity	0.587	0.052

Fixed effects	Wald stat.	n.d.f.	F	d.d.f.	F pr
Contrast monoculture/mixture (M)	**6.33**	**1**	**6.33**	**213.4**	**0.013**
Plot size	0.03	1	0.03	293.9	0.855
Log_2(species richness (SR))	0.24	1	0.24	91.3	0.625
SR (deviation from log-linearity)	3.69	2	1.84	102.2	0.164
Functional group (FG) identity	1.86	3	0.62	49.6	0.606
M x FG identity	8.96	3	2.99	348.9	0.031
Plot size x FG identity	0.21	3	0.07	294.4	0.976
Log_2(SR) x FG identity	5.20	3	1.73	374.3	0.160
SR x FG identity	5.87	6	0.98	369.3	0.440

Table 1b

Variance components for random terms	Estimate	s.e.
Block	0.003	0.012
Plot	0.051	0.039
Species identity	0.239	0.072
Residual = Plot x species identity	0.985	0.075

Fixed effects	Wald stat.	n.d.f.	F	d.d.f.	F pr
Contrast monoculture/mixture (M)	**10.13**	**1**	**10.13**	**338.6**	**0.002**
Plot size	0.03	1	0.03	423.9	0.859
Log_2(species richness (SR))	0.00	1	0.00	90.7	0.979
SR (deviation from log-linearity)	1.77	2	0.88	98.6	0.417
Functional group (FG) identity	0.98	3	0.33	53.9	0.807
M x FG identity	3.65	3	1.22	426.0	0.303
Plot size x FG identity	1.70	3	0.57	423.4	0.637
Log_2(SR) x FG identity	0.29	3	0.10	400.4	0.961
SR x FG identity	3.94	6	0.66	400.6	0.685

Table 2. Mean annual relative growth rates ± 1 standard error per species and per functional group growing in mixture (Δ Mix) or in monoculture (Δ Mono), for the time intervals 2003–2005 and 2005–2007. Species are ordered according to their functional group identity. The asterisks following the mean values per functional group indicate significant differences from zero; n. s. stands for non significant. If no standard error is given, the annual relative growth rate was obtained from a single observation. Nomenclature follows Rothmaler (2002).

	2003–2005		2005–2007	
Species	**Δ Mix**	**Δ Mono**	**Δ Mix**	**Δ Mono**
Alopecurus pratensis	-0.04 ± 0.13	-0.31 ± 0.14	-0.07 ± 0.12	0.12 ± 0.04
Anthoxanthum odoratum	-0.90 ± 0.56	-0.61 ± 0.09	0.08 ± 0.42	0.32 ± 0.06
Arrhenatherum elatius	-0.79 ± 0.14	-0.27 ± 0.10	0.05 ± 0.14	-0.56 ± 0.02
Avenula pubescens	0.68 ± 0.63	-0.33 ± 0.05	0.26 ± 0.57	-0.11 ± 0.21
Bromus erectus	-0.20 ± 0.38	-0.66 ± 0.08	1.03 ± 0.40	0.17 ± 0.04
Bromus hordeaceus	-0.55 ± 0.47	-0.30 ± 0.14	0.40 ± 0.31	0.03 ± 0.01
Cynosurus cristatus	-0.05	0.22 ± 0.12	-1.91	-0.75 ± 0.57
Dactylis glomerata	-0.33 ± 0.16	-0.65 ± 0.50	0.18 ± 0.02	0.33 ± 0.51
Festuca pratensis	-0.93 ± 0.34	-0.79 ± 0.26	0.82 ± 0.42	0.27 ± 0.17
Festuca rubra	-0.31 ± 0.12	-0.60 ± 0.15	0.25 ± 0.20	0.48 ± 0.10
Holcus lanatus	-0.93 ± 0.54	-0.15 ± 0.12	-0.23 ± 0.72	0.19 ± 0.07
Luzula campestris	n. a.	n. a.	1.35 ± 0.98	n. a.
Phleum pratense	-0.77 ± 0.19	-0.51 ± 0.01	-0.64 ± 0.26	0.15 ± 0.13
Poa pratensis	-0.18 ± 0.32	-0.38 ± 0.08	0.44 ± 0.18	0.41 ± 0.06
Poa trivialis	-1.31 ± 0.34	-0.48 ± 0.04	1.15 ± 0.29	-0.51 ± 0.33
Trisetum flavescens	0.18 ± 0.16	-0.24 ± 0.00	0.06 ± 0.07	-0.25 ± 0.47
Grasses	**-0.46 ± 0.10 *****	**-0.40 ± 0.06 *****	**0.29 ± 0.10 ****	**0.03 ± 0.09 n. s.**
Ajuga reptans	1.29 ± 0.21	-0.17 ± 0.21	0.38 ± 0.46	-1.67
Bellis perennis	0.33 ± 0.24	0.00 ± 0.10	-0.27 ± 0.75	0.80 ± 1.10
Glechoma hederacea	-0.22 ± 0.21	-1.10 ± 0.22	-0.17 ± 0.23	-0.04 ± 0.80
Leontodon autumnalis	-0.21 ± 0.53	-0.68 ± 0.16	-0.72 ± 0.43	-0.06 ± 0.07
Leontodon hispidus	0.47 ± 0.27	-0.40 ± 0.07	0.92 ± 0.25	0.14 ± 0.03
Plantago lanceolata	-1.22 ± 0.27	-0.71 ± 0.20	1.15 ± 0.20	0.51 ± 0.16
Plantago media	0.08 ± 0.20	-0.78 ± 0.01	0.76 ± 0.12	0.37 ± 0.00
Primula veris	n. a.	1.35 ± 0.18	1.77 ± 0.65	-0.43 ± 0.31
Prunella vulgaris	-0.07 ± 0.56	-1.47 ± 0.09	-0.85 ± 0.96	0.44 ± 0.23
Ranunculus repens	-0.42 ± 0.39	-0.88 ± 0.24	0.98 ± 0.47	0.41 ± 0.00
Taraxacum officinale	-0.32 ± 0.12	-0.29 ± 0.12	-0.26 ± 0.17	-0.20 ± 0.01
Veronica chamaedrys	0.66 ± 0.10	-0.27 ± 0.02	0.53 ± 0.15	0.03 ± 0.23
Small herbs	**-0.14 ± 0.11 n. s.**	**-0.47 ± 0.13 ****	**0.43 ± 0.13 ****	**0.13 ± 0.13 n. s.**
Achillea millefolium	-0.77 ± 0.22	-0.75 ± 0.06	-0.16 ± 0.22	-0.09 ± 0.05
Anthriscus sylvestris	1.55 ± 1.21	1.00 ± 0.13	2.19 ± 1.02	-0.93 ± 0.27
Campanula patula	-1.39	-0.78	1.46	-0.99
Carum carvi	-0.81 ± 0.35	-1.14 ± 0.25	1.32 ± 0.98	0.50 ± 0.08
Cardamine pratensis	n. a.	n. a.	n. a.	n. a.
Centaurea jacea	-0.27 ± 0.12	-0.62 ± 0.04	-0.03 ± 0.25	-0.18 ± 0.24
Cirsium oleraceum	-0.79 ± 0.28	-0.60 ± 0.02	0.03 ± 0.96	-0.05 ± 0.09
Crepis biennis	-0.77 ± 0.40	-0.85 ± 0.06	0.55 ± 0.40	0.01 ± 0.26
Daucus carota	-1.21 ± 0.23	-0.42 ± 0.01	-0.03 ± 0.17	-0.64 ± 0.04
Galium mollugo	0.71 ± 0.11	-0.34 ± 0.09	0.48 ± 0.19	-0.08 ± 0.09
Geranium pratense	0.37 ± 0.25	-0.09 ± 0.13	0.70 ± 0.36	-0.39 ± 0.18

Heracleum sphondylium	1.77 ± 0.77	1.40 ± 0.28	1.72 ± 0.45	-0.10 ± 0.25
Knautia arvensis	0.09 ± 0.20	-0.69 ± 0.06	0.14 ± 0.13	0.23 ± 0.08
Leucanthemum vulgare	-0.39 ± 0.08	-0.74 ± 0.01	-0.22 ± 0.17	0.34 ± 0.15
Pastinaca sativa	n. a.	-0.45 ± 0.10	1.43 ± 0.40	0.35 ± 0.05
Pimpinella major	-0.04 ± 0.45	-0.41 ± 0.25	1.38 ± 0.27	0.03 ± 0.06
Ranunculus acris	0.31 ± 0.24	-0.27 ± 0.04	-0.18 ± 0.57	0.02 ± 0.18
Rumex acetosa	-0.46 ± 0.23	-0.77 ± 0.11	-0.08 ± 0.24	0.02 ± 0.13
Sanguisorba officinalis	1.04	0.26 ± 0.11	0.40 ± 0.99	-0.27 ± 0.08
Tragopogon pratensis	-1.01 ± 0.29	-0.52 ± 0.02	-0.76 ± 0.91	-0.17 ± 0.13
Tall herbs	**-0.11 ± 0.12 n. s.**	**-0.36 ± 0.10 *****	**0.56 ± 0.14 *****	**-0.10 ± 0.07 n. s.**
Lathyrus pratensis	1.45 ± 0.66	-0.06 ± 0.09	0.90 ± 0.36	-0.29 ± 0.31
Lotus corniculatus	0.31 ± 0.19	-0.53 ± 0.33	-0.35 ± 0.21	-0.10 ± 0.08
Medicago lupulina	-0.27 ± 0.41	0.05 ± 0.16	-1.15 ± 1.09	0.56 ± 0.12
Medicago x varia	0.14 ± 0.15	-0.18 ± 0.08	-0.18 ± 0.19	-0.33 ± 0.22
Onobrychis viciifolia	-0.10 ± 0.1	-0.03 ± 0.11	0.23 ± 0.08	-0.07 ± 0.20
Trifolium campestre	-0.24	-0.52 ± 1.60	2.10 ± 0.60	2.00 ± 0.40
Trifolium dubium	n. a.	2.27	0.77 ± 0.72	2.75
Trifolium fragiferum	2.50 ± 0.74	-0.01	1.16 ± 0.22	0.44
Trifolium hybridum	-1.69 ± 0.18	-1.13 ± 0.07	0.32 ± 0.58	-0.86 ± 0.51
Trifolium pratense	-0.70 ± 0.16	-0.10 ± 0.52	0.14 ± 0.46	0.09 ± 0.14
Trifolium repens	-1.78 ± 0.48	-0.40 ± 0.10	1.48 ± 0.59	0.21 ± 0.04
Vicia cracca	-0.37 ± 0.31	-0.54 ± 1.24	0.46 ± 0.26	0.61 ± 0.49
Legumes	**-0.25 ± 0.15 n. s.**	**-0.20 ± 0.17 n. s.**	**0.39 ± 0.16 ***	**0.24 ± 0.18 n. s.**

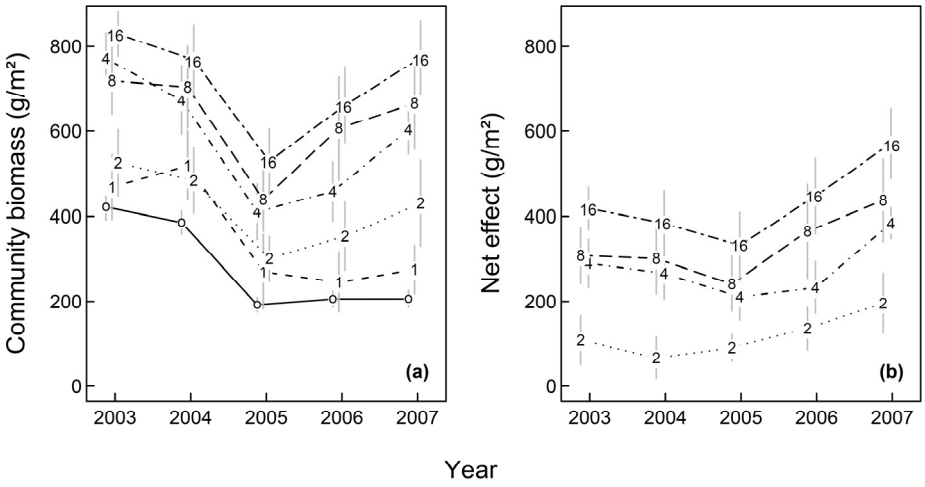

Fig. 1. Aboveground community biomass (a) and net effect (b) in the years 2003–2007. Symbols indicate means per species richness level ± 1 standard error (in (a), "o" indicates monocultures of small plot size). Symbols were slightly jittered to improve visualization.

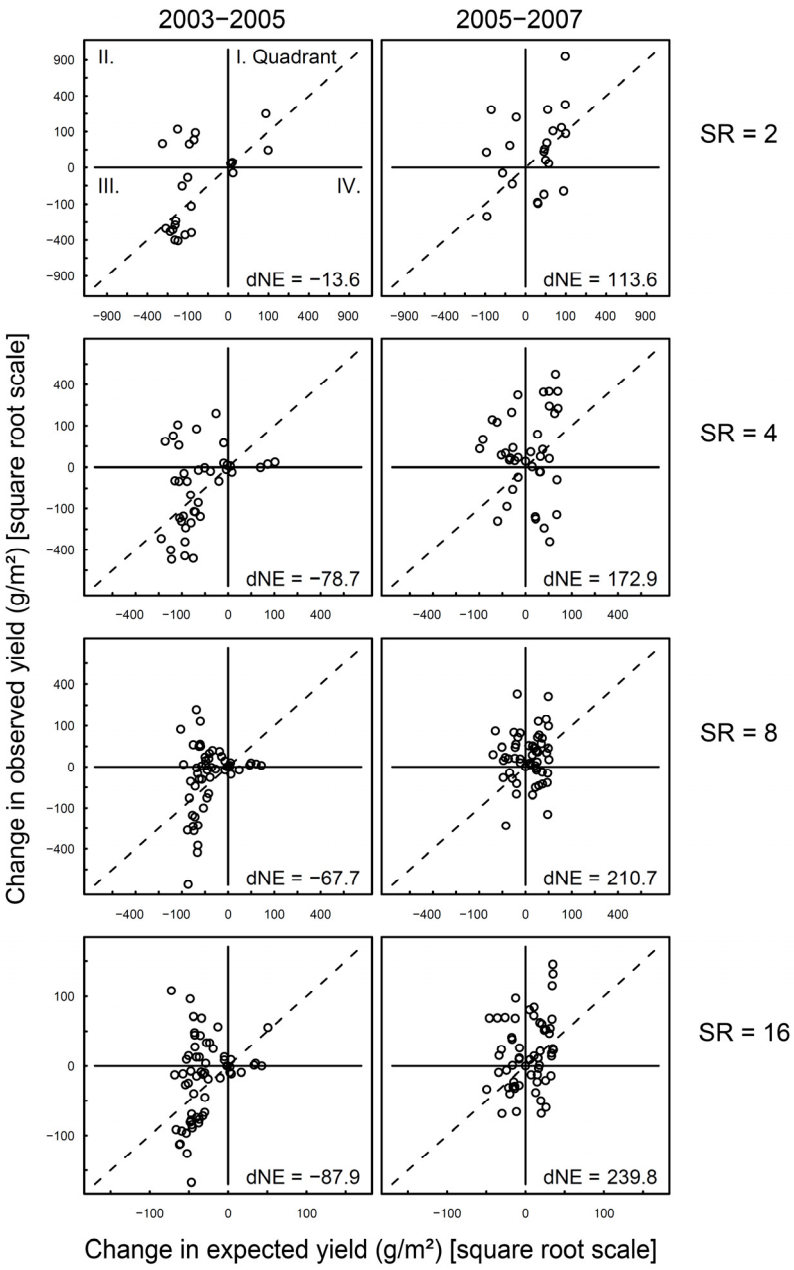

Fig. 2. Relationship between mean changes in expected yield and mean changes in observed yield per species for the time intervals 2003–2005 and 2005–2007, separated according to species richness level. A point falling on the solid vertical line indicates that a species has not changed in its expected yield (i.e., in monoculture) in the respective time interval. A point falling on the solid horizontal line indicates that a species has not changed in its observed yield (i.e., in mixture) in the respective time interval. A point falling below the broken diagonal line contributed to a decline in the net effect and a point falling above the broken diagonal line contributed to an increase in the net effect. "dNE" indicates the absolute change in the net effect (in g/m^2) that occurred on average at the corresponding species richness level within the respective time interval. Note the square-root scale and the different ranges of the axes. The number of data points differs between the diversity levels because the number of species represented in the communities increased with increasing species richness.

Chapter 3

The Jena-Experiment: 6 years of data from a grassland biodiversity experiment including species-specific plant biomass, species-specific plant cover, community LAI and community height.

Alexandra Weigelt, Elisabeth Marquard, Vicky M. Temperton, Christiane Roscher, Christoph Scherber, Peter N. Mwangi, Nina Buchmann, Bernhard Schmid, Ernst-Detlef Schulze & Wolfgang W. Weisser (Manuscript submitted to *Ecological Archives*)

Abstract

This data set contains species-specific biomass and cover data as well as community leaf area index (LAI) and height from a large grassland biodiversity experiment (Jena Experiment). In this experiment, 82 grassland plots of 20 x 20 m were established from a pool of 60 species belonging to four functional groups (grasses, legumes, tall and small herbs). In May 2002, varying numbers of plant species were sown into the plots to create a gradient of plant species richness (1, 2, 4, 8, 16 and 60 species) and functional richness (1, 2, 3, 4 functional groups). Plots were maintained by bi-annual weeding and mowing. The data set encompasses the 2002 to 2008 May and August biomass harvests from 3–4 subplots of 0.2 x 0.5 m per experimental plot sorted to species. Moreover, plant species and community cover estimated in an approximately 9 m² subplot per plot are included in the dataset. Each biomass harvest was accompanied by measurements of vegetation height and LAI per plot. Analyses of the community biomass data have identified species richness as well as functional group composition as important drivers of a positive biodiversity–productivity relationship (Marquard *et al.* 2009).

The data set can be used to study a variety of questions about how plant community composition and structure responds to changes in species richness and functional diversity over time. Sampling is ongoing, and new data will be added in 2010.

Keywords

Biodiversity experiment, species biomass, LAI, height, species cover, functional composition, plant community

Research Origin Descriptors

All data included in this dataset were measured on the experimental grassland plots of the Jena Experiment from 2002 to 2008. The Jena Experiment is funded by the Deutsche Forschungsgemeinschaft (DFG, FOR 456), with additional support from the Friedrich Schiller University of Jena, the Max Planck Society, the University of Zurich, and the Swiss National Science Foundation (grant 3100AO-107531 to B. Schmid). Only parts of the dataset have been published so far. This includes mean plot biomass from May 2003 (Roscher *et al.* 2005), from August 2003 and May 2004 (Beßler *et al.* 2009), annual species-specific and mean plot biomass from 2003 to 2007 (Marquard *et al.* 2009; Marquard *et al.* in prep.), annual mean biomass from 2003 alone (Scherber *et al.* 2006) and from 2006 alone (Eisenhauer *et al.* 2009; Eisenhauer *et al.* submitted), biomass of one subsample from May and August 2003 and 2004 (Roscher *et al.* 2009b), biomass of all subsamples from August 2005 (Weigelt *et al.* 2008), mean plot biomass of one or three experimental blocks, respectively, from May and August 2003 and 2004 (Oelmann *et al.* 2007a; Oelmann *et al.* 2007b), and species-specific biomass of the 60-species mixtures from May and August 2005 to 2007 (Petermann *et al.* 2009). LAI, community height and species-specific cover over all years have not been used in publications so far except for cover of sown species from May 2004 (Roscher *et al.* 2009a). The following people have contributed to the data included in this file: biomass 2002–2004 (Vicky Temperton/Nina Buchmann), biomass 2005–2008 (Alexandra Weigelt), LAI 2003–2004 (Vicky Temperton/Nina Buchmann), height August 2002 (Vicky Temperton/Nina Buchmann), height August 2003 (Christoph Scherber/Wolfgang Weisser), height May 2004 (Peter Mwangi/Bernhard Schmid), LAI and height 2005–2008 (Alexandra Weigelt), species cover 2002–2004 and 2008 (Christiane Roscher), species cover 2005–2007 (Elisabeth Marquard/Bernhard Schmid). Those in the best position to answer questions concerning the data are Alexandra Weigelt (alexandra.weigelt@uni-jena.de), Elisabeth Marquard (lisa.marquard@uwinst.uzh.ch) and Christiane Roscher (croscher@bgc-jena.mpg.de), those in the best position to answer questions concerning the experimental design are Jens Schumacher (jschum@minet.uni-jena.de) and Bernhard Schmid (bernhard.schmid@uwinst.unizh.ch).

Data set description

The metadata presented here correspond to the comma-separated-value data files named:

‘Jena_ Biomass_02-08.csv’

‘Jena_ Community_02-08.csv’.

Cells noted with "NA" indicate that the information is not reported, or not available from these plots or at the times.

Column numbers; headings and descriptions for file: 'Jena_ Biomass_02-08.csv'

Column no.	Header	Description	Unit
1	Plotcode	Complete code of experimental plot	
2	Block	Identification (ID) of the block (1–4 blocks)	
3	Plot	ID of the plot	
4	subsample	ID of the subsample (3 or 4 subsamples per plot)	
5	Year	Year of sampling	
6	Month	Month of sampling	
7	Time	Number of months after start of the experiment (1 = May 2002)	
8	X	X-coordinate of 0/0 corner per large plot on a grid of the field site (see Fig. 1)	m
9	Y	Y-coordinate of 0/0 corner per large plot on a grid of the field site (see Fig. 1)	m
10	x	x-coordinate of subsample in each large plot (see Fig. 1)	cm
11	y	y-coordinate of subsample in each large plot (see Fig. 1)	cm
12	sowndiv	Number of species sown per plot	
13	numfg	Number of functional groups sown per plot	
14	numgrass	Number of grass species sown per plot	
15	numsherb	Number of small herb species sown per plot	
16	numtherb	Number of tall herb species sown per plot	
17	numleg	Number of legume species sown per plot	
18	gr.ef	Presence of grasses, 0=no, 1=yes	
19	sh.ef	Presence of small herbs, 0=no, 1=yes	
20	th.ef	Presence of tall herbs, 0=no, 1=yes	
21	leg.ef	Presence of legumes, 0=no, 1=yes	
22	Unidentified.Rest	Sum of dry weight of unidentified parts OR sum of dry weight of species not belonging to the target species pool on special plots (free succession, succession with mowing, reference plots)	g m-2
23	DOM	Dry weight of dead organic material	g m-2
24	target.biomass	Sum of all sown species dry weights per subplot OR sum of dry weight of all species belonging to the target species pool on special plots (free succession, succession with mowing, reference plots)	g m-2
25–84		Dry weight of single species	
25	Alo.pra	*Alopecurus pratensis*	g m-2
26	Ant.odo	*Anthoxanthum odoratum*	g m-2
27	Arr.ela	*Arrhenatherum elatius*	g m-2
28	Ave.pub	*Avenula pubescens*	g m-2

29	Bro.ere	*Bromus erectus*	g m-2
30	Bro.hor	*Bromus hordeaceus*	g m-2
31	Cyn.cri	*Cynosurus cristatus*	g m-2
32	Dac.glo	*Dactylis glomerata*	g m-2
33	Fes.pra	*Festuca pratensis*	g m-2
34	Fes.rub	*Festuca rubra*	g m-2
35	Hol.lan	*Holcus lanatus*	g m-2
36	Luz.cam	*Luzula campestris*	g m-2
37	Phl.pra	*Phleum pratense*	g m-2
38	Poa.pra	*Poa pratensis*	g m-2
39	Poa.tri	*Poa trivialis*	g m-2
40	Tri.fla	*Trifolium fragiferum*	g m-2
41	Aju.rep	*Ajuga reptans*	g m-2
42	Bel.per	*Bellis perennis*	g m-2
43	Gle.hed	*Glechoma hederacea*	g m-2
44	Leo.aut	*Leontodon autumnalis*	g m-2
45	Leo.his	*Leontodon hispidus*	g m-2
46	Pla.lan	*Plantago lanceolata*	g m-2
47	Pla.med	*Plantago media*	g m-2
48	Pri.ver	*Primula veris*	g m-2
49	Pru.vul	*Prunella vulgaris*	g m-2
50	Ran.rep	*Ranunculus repens*	g m-2
51	Tar.off	*Taraxacum officinale*	g m-2
52	Ver.cha	*Veronica chamaedrys*	g m-2
53	Ach.mil	*Achillea millefolium*	g m-2
54	Ant.syl	*Anthriscus sylvestris*	g m-2
55	Cam.pat	*Campanula patula*	g m-2
56	Car.pra	*Cardamine pratensis*	g m-2
57	Car.car	*Carum carvi*	g m-2
58	Cen.jac	*Centaurea jacea*	g m-2
59	Cir.ole	*Cirsium oleraceum*	g m-2
60	Cre.bie	*Crepis biennis*	g m-2
61	Dau.car	*Daucus carota*	g m-2
62	Gal.mol	*Galium mollugo*	g m-2
63	Ger.pra	*Geranium pratense*	g m-2
64	Her.sph	*Heracleum sphondylium*	g m-2
65	Kna.arv	*Knautia arvensis*	g m-2
66	Leu.vul	*Leucanthemum vulgare*	g m-2
67	Pas.sat	*Pastinaca sativa*	g m-2
68	Pim.maj	*Pimpinella major*	g m-2
69	Ran.acr	*Ranunculus acris*	g m-2
70	Rum.ace	*Rumex acetosa*	g m-2
71	San.off	*Sanguisorba officinalis*	g m-2
72	Tra.pra	*Tragopogon pratensis*	g m-2
73	Lat.pra	*Lathyrus pratensis*	g m-2
74	Lot.cor	*Lotus corniculatus*	g m-2
75	Med.lup	*Medicago lupulina*	g m-2

76	Med.var	*Medicago x varia*	g m-2
77	Ono.vic	*Onobrychis viciifolia*	g m-2
78	Tri.cam	*Trifolium campestre*	g m-2
79	Tri.dub	*Trifolium dubium*	g m-2
80	Tri.fra	*Trifolium hybridum*	g m-2
81	Tri.hyb	*Trifolium pratense*	g m-2
82	Tri.pra	*Trifolium repens*	g m-2
83	Tri.rep	*Trisetum flavescens*	g m-2
84	Vic.cra	*Vicia cracca*	g m-2

Column numbers; headings and descriptions for file: 'Jena_ Community_02-08.csv'

Column no.	**Header**	**Description**	**Unit**
1	Plotcode	Complete code of experimental plot	
2	Block	Identification (ID) of the block (1–4 blocks)	
3	Plot	ID of the plot	
4	Year	Year of sampling	
5	Month	Month of sampling	
6	Time	Number of months after start of the experiment (1 = May 2002)	
7	X	X-coordinate of 0/0 corner per large plot on a grid of the field site (see Fig. 1)	m
8	Y	Y-coordinate of 0/0 corner per large plot on a grid of the field site (see Fig. 1)	m
9	sowndiv	Number of species sown per plot	
10	numfg	Number of functional groups sown per plot	
11	numgrass	Number of grass species sown per plot	
12	numsherb	Number of small herb species sown per plot	
13	numtherb	Number of tall herb species sown per plot	
14	numleg	Number of legume species sown per plot	
15	gr.ef	Presence of grasses, 0=no, 1=yes	
16	sh.ef	Presence of small herbs, 0=no, 1=yes	
17	th.ef	Presence of tall herbs, 0=no, 1=yes	
18	leg.ef	Presence of legumes, 0=no, 1=yes	
19	LAI	Community leaf area index (LAI) given as mean over 10 separate measurement taken along a transect of 10 m length	
20	SEL (LAI)	Standard error of mean LAI for single measurements	
21	DIFN (LAI)	Diffuse non-interceptance (fraction of sky visible to the sensor)	
22	MTA (LAI)	Mean tilt angle in degrees	degrees
23	SEM (LAI)	Standard error of MTA	
24	SMP (LAI)	Number of pairs of above and below observations that were included in the calculations	

25	Mean Height Veg	Mean over column 25–34; 10 separate measurements of highest leaves taken along a transect of 10 m length at 1 m distances	m
26	Mean Height Flo	Mean over column 35–44; 10 separate measurements of highest flower (if present) taken along a transect of 10 m length at 1 m distances	m
27	Height 1 Veg	Height of highest leaf of randomly chosen target individual at meter 1 of a 10 m transect	m
28	Height 2 Veg	Height of highest leaf of randomly chosen target individual at meter 2 of a 10 m transect	m
29	Height 3 Veg	Height of highest leaf of randomly chosen target individual at meter 3 of a 10 m transect	m
30	Height 4 Veg	Height of highest leaf of randomly chosen target individual at meter 4 of a 10 m transect	m
31	Height 5 Veg	Height of highest leaf of randomly chosen target individual at meter 5 of a 10 m transect	m
32	Height 6 Veg	Height of highest leaf of randomly chosen target individual at meter 6 of a 10 m transect	m
33	Height 7 Veg	Height of highest leaf of randomly chosen target individual at meter 7 of a 10 m transect	m
34	Height 8 Veg	Height of highest leaf of randomly chosen target individual at meter 8 of a 10 m transect	m
35	Height 9 Veg	Height of highest leaf of randomly chosen target individual at meter 9 of a 10 m transect	m
36	Height 10 Veg	Height of highest leaf of randomly chosen target individual at meter 10 of a 10 m transect	m
37	Height 1 Flo	Height of highest flower (if present) of the same randomly chosen target individual as for column 27	m
38	Height 2 Flo	Height of highest flower (if present) of the same randomly chosen target individual as for column 28	m
39	Height 3 Flo	Height of highest flower (if present) of the same randomly chosen target individual as for column 29	m
40	Height 4 Flo	Height of highest flower (if present) of the same randomly chosen target individual as for column 30	m
41	Height 5 Flo	Height of highest flower (if present) of the same randomly chosen target individual as for column 31	m
42	Height 6 Flo	Height of highest flower (if present) of the same randomly chosen target individual as for column 32	m
43	Height 7 Flo	Height of highest flower (if present) of the same randomly chosen target individual as for column 33	m
44	Height 8 Flo	Height of highest flower (if present) of the same randomly chosen target individual as for column 34	m
45	Height 9 Flo	Height of highest flower (if present) of the same randomly chosen target individual as for column 35	m
46	Height 10 Flo	Height of highest flower (if present) of the same randomly chosen target individual as for column 36	m
47	cover.target	Proportion of total area that is covered by sown species per estimated plot area	%
48	cover.weeds	Proportion of total area that is covered by non-sown species per estimated plot area	%

49	cover.bare.ground	Proportion of total area that is covered by bare ground per estimated plot area	%
50	cover.dead	Proportion of total area that is covered by dead material per estimated plot area	%
51–111	Single species	Cover estimates of single species (abbreviations as given for data table 1) per estimated plot area	%

Methods

We encourage users of this dataset to read the detailed methods that have appeared in Roscher *et al.* (2004) and Marquard *et al.* (2009) and other papers cited above.

DESCRIPTION OF THE STUDY AREA AND EXPERIMENTAL DESIGN

The field site of the Jena Experiment encompasses approx. 10 ha of former agricultural land in the floodplain of the river Saale near Jena (Germany, 50°55' N, 11°35' E, 130 m altitude). The area around Jena is characterized by a mean annual air temperature of 9.3 °C, and a mean annual precipitation of 587 mm (Kluge & Müller-Westermeier 2000). The soil consists of sandy loam in the vicinity of the river which gradually changes to silty clay with increasing distance from the river.

In May 2002, 82 plant assemblages of common Central European grassland species were sown with a total of 1000 viable seeds per m² on plots of 20 x 20 m that had been kept fallow in the year before sowing, harrowed bimonthly and treated with glyphosate (Roundup, Monsanto company, St. Louis, Missouri USA) in July 2001. Species compositions were determined by constrained random selection from a pool of 60 species. Based on a cluster analysis of ecological and morphological traits, these 60 target species had been assigned to four functional groups: 16 grasses, 12 small herbs, 20 tall herbs and 12 legumes. In mixtures, all species were sown with equal proportions and in plots with more than one functional group all functional groups were sown as evenly as possible (Roscher *et al.* 2004). Table 1 in Marquard *et al.* (2009) shows the sown levels of species richness and functional group richness as well as the sown proportions of each functional group at the different diversity levels. Species richness, functional group richness and the presence of the functional groups were varied as orthogonally as possible. However, there were not enough legumes and small herbs in the overall species pool to assemble them in mixtures with 16 species of the same functional group. Each functional group was sown in four monocultures, six 2-species mixtures, ten 4-species mixtures, ten 8-species mixtures and nine or ten 16-species mixtures

which resulted in the presence of each functional group on 43 (legumes and small herbs) or 44 (tall herbs and grasses) of the 82 plots.

All experimental plots were maintained without fertilizer application and mown twice a year (in early June and early September). Species occurring on plots where they had not been sown were removed during biannual weeding campaigns (at the beginning of the growing season and after the first mowing). Weeding was mainly done by hand; herbicides were used where target species composition allowed their application (herbicides against dicotyledonous plants in pure grass communities and against grasses on plots with herbs only). Empirical data showed that the application of herbicides did not affect the relationship between biodiversity and aboveground community biomass: on each of our grassland plots, a small subplot was only weeded and never treated with herbicides. These subplots showed the same biodiversity–productivity relationship as observed on the remaining area of the plots (Roscher *et al.* 2009b). The weeding treatment however might have decreased or increased the biodiversity–productivity relationship to some extent because low-diversity plots had to be weeded more intensively than high-diversity plots (Weigelt, unpublished data).

We also included data of 6 additional 20 x 20 m plots not belonging to the main biodiversity gradient. These are four succession plots which received the same soil preparations as all other large plots in 2001 (fallow land, harrowing, glyphosate treatment) but no sowing of plant species in May 2002. Two of these four plots are mown twice a year together with the rest of the experimental plots (succession with mowing) and two are left without mowing (free succession). In addition, one plot on each of two managed grasslands less than 100 m north and south of the field site were measured (reference plots). These grasslands are mown twice a year in early June and September by a local farmer and receive no fertilizer. All additional plots were not weeded.

The field site was divided into four blocks to account for altering soil and water conditions. Plots of all diversity levels were distributed in nearly equal shares across all four blocks. Weeding, mowing and herbicide application were completed blockwise in rotating order.

Each 20 x 20 m plot was subdivided according to Fig. 1.

RESPONSE VARIABLES

Biomass harvest: Aboveground community biomass was harvested in September 2002 and from 2003–2008 twice a year (during peak standing biomass in late May and in late August)

on all experimental plots. This was done by clipping the vegetation at 3 cm above ground in four (in May 2005 and from August 2007 onwards only three) rectangles of 0.2 x 0.5 m per large plot. The location of these rectangles was assigned prior to each harvest by random selection of coordinates (given as x and y coordinates in file 'Jena_ Biomass_02-08.csv') within the core area of the plots (Fig. 1). The positions of the rectangles within plots were identical for all plots at a particular harvest. The harvested biomass was sorted into target species (species sown at the particular plot), total weeds (species not sown at the particular plot) and detached dead organic material and dried to constant weight (70° C, ≥ 48 h). In August 2004, the harvested biomass samples were not sorted into species (they were only sorted into legumes and non-legumes; data not reported). For all biomass harvests in 2003 and 2004 the biomass subsample number 4 was collected in an extra carefully weeded subplot of the core area.

LAI measurement: Community leaf area index (LAI) was measured twice a year just before biomass harvest (during peak standing biomass in late May and in late August) from 2003 to 2008 with a LAI-2000 plant canopy analyzer (LI-COR) using high resolution and a view cap masking 45° of the azimuth towards the operator. In 2003 and 2004, 10 randomly allocated measurements were taken at 5 cm height (i.e. the height of the lens above the ground when the sensor was placed on the ground) within an area of 3 x 3 m in the center of the core area (Fig. 1). From 2005 onwards all measurements were taken along a 10 m transect (Fig. 1) in the core area of each experimental plot. One above reading was taken at the first transect point, followed by 10 below readings taken at 5 cm height and with 1 m distance from each other. Given in the dataset is the mean over the 10 calculated LAI values from the below readings as mean community LAI per plot.

Vegetation height: Plant height was measured twice a year just before biomass harvest (during peak standing biomass in late May and in late August) concurrently to LAI from 2002 to 2008, except for May 2003 and August 2004. In August 2002, stretched height of 3 target plant individuals (if present) per sown species was measured in the core area of each experimental plot (Fig. 1). Given is mean stretched height over all species measured per plot. In August 2003, 30 target plant individuals were harvested at 10 cm distances along a 5 m transect in a control area (no additional treatments) at the margin of each experimental plot (Fig. 1). Given is the mean length of the main axis for these 30 individuals. In May 2004, apparent height was measured at three points in another control area at the margin of each experimental plot (Fig. 1). From 2005 onwards all measurements were taken along a 10 m

transect (Fig. 1) in the core area of each experimental plot using a rule. Apparent height of the highest leaf and flower (if present) of the same target plant individual was recorded at 10 points along the transect separated by 1 m each. The community data table gives all individual measurements as well as the mean apparent community height.

Species and community cover: Sown species cover was visually estimated twice a year just before biomass harvest (during peak standing biomass in late May and in late August) from 2003 to 2008 and in September 2002. Community cover data (columns 47–50) were estimated directly as percentages. Single species cover (columns 51–111) were estimated using the cover classes given below. From 2002 to 2004, measurements were taken in two extra carefully weeded sub-areas of 2 x 2.25 m (Fig. 1). We report the average value based on these two estimates for community cover (columns 47–50). For single species cover, we report the smaller of the two estimates in cover classes as conservative measure if cover values differed by only one cover class between sub-areas and the intermediate cover class if cover values differed by two cover classes between sub-areas (columns 51–111). From 2005 onwards all measurements were taken in one 3 x 3 m area in the core area of each experimental plot (Fig. 1). 0 = species missing; **1**: < 1%; **2**: 1 % ≤ x < 5%; **10**: 5 % ≤ x < 15%; **20**: 15 % ≤ x < 25%; **30**: 25 % ≤ x < 35%; **40**: 35 % ≤ x < 45%; **50**: 45 % ≤ x < 55%; **60:** 55 % ≤ x < 65%; **70**: 65 % ≤ x < 75%; **80**: 75 % ≤ x < 85%; **90**: ≥ 85%. See below for comments on weed cover.

Weed biomass and cover: In the file 'Jena_Community_02-08.csv' column 48 give the cover of weed species, e.g. all non-sown species per plot. This data is included as a measure of weed pressure shortly before biomass harvest, but it is no standardized measurement and we strongly advise users to handle this variable with care for two reasons: (1) the large area of experimental plots in the Jena Experiment leads to weeding periods of 3–5 weeks depending on weather conditions. (2) Increasing weed pressure over time made it sometimes impossible to weed all plots twice a year, especially when unfavorable weather conditions restricted the time frame when weeding was possible (wet soil conditions and high vegetation would have caused too much damage if weeding would have been carried out). Therefore plot specific time between last weeding and vegetation cover estimates varies from 3–8 weeks or even up to a year depending on the time when the plot was last weeded.

Data-use policy

The data presented here are publicly available. Those wishing to publish results from this dataset should read this meta-data document. The data set should be cited as: Weigelt,

Marquard, Temperton, Roscher, Scherber, Mwangi, Buchmann, Schmid, Schulze, Weisser (2009) The Jena-Experiment: 6 years of data from a grassland biodiversity experiment including species-specific plant biomass, species-specific plant cover, community LAI and community height. Ecological Archives, XXX.

The following analyses using either species-specific biomass or cover data from 2003 to 2008 are in preparation:

1. Biodiversity and sustaining ecosystem functioning across several years. E. Allen, W. W. Weisser, H. Hillebrand *et al.* This paper will test for temporal multifunctionality, i.e. if more species are required to maintain functioning across several subsequent years. We analysed species-specific biomass data, calculating the number of species required to ensure 50% of biomass productivity per plot for single years and for multiple years.

2. How abiotic and biotic filters influence phylogenetic dispersion in grassland communities. E. Allen, A. Fergus, T. Jenkins, B. Schmid *et al.* This approach tests if communities which have been randomly assembled initially, become increasingly phylogenetically structured with time. We will calculate phylogenetic diversity based on abundance data for each plot in each year.

3. Stability in space and time: a case study using plant biomass. R. Proulx, E. Allan, A. Weigelt *et al.* In this approach we calculate determinism and multivariate CV using species-specific biomass over time to see if biomass stability in space, between seasons (May and August) and between years changes with increasing diversity of the plant community.

4. Plant traits as predictors for species yields in experimental grasslands. C. Roscher, A. Lipowsky, M. Gubsch, N. Buchmann, B. Schmid, E.-D. Schulze *et al.*. In this study we analyse morphological, ecophysiological and demographic plant traits measured for all species in monocultures and mixtures as predictors for species yields, its temporal changes including weather data and explore the role of plant functional trait plasticity.

5. Relationships between mean plant functional traits, functional trait diversity and ecosystem processes. C. Roscher, J. Schumacher, A. Lipowsky, M. Gubsch, N. Buchmann, B. Schmid, E.-D. Schulze *et al.* Using a method based on Rao's quadratic diversity (Schumacher & Roscher 2009) we assess the importance of abundance-weighted mean trait values and functional trait diversity. This analysis uses plant functional traits measured in monocultures and species mixtures and incorporates trait plasticity.

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Chapter references

Beßler H., Temperton V. M., Roscher C., Buchmann N., Schmid B., Schulze E.-D., Weisser W. W. & Engels C. (2009). Aboveground overyielding in experimental grassland mixtures is related to altered biomass partitioning to belowground organs. *Ecology*, accepted.

Eisenhauer N., Beßler H., Engels C., Gleixner G., Habekost M., Milcu A., Partsch S., Sabais A. C. W., Scherber C., Steinbeiss S., Weigelt A., Weisser W. W. & Scheu S. (2009). Plant diversity effects on soil microorganisms support the singular hypothesis. *Ecology*, in revision.

Eisenhauer N., Milcu A., Sabais A. C. W., Beßler H., Weigelt A., Engels C. & Scheu S. (submitted). Plant community impacts on the structure of earthworm communities depend on season. *Biology and Biochemistry*.

Kluge G. & Müller-Westermeier G. (2000). *Das Klima ausgewählter Orte der Bundesrepublik Deutschland: Jena*. Deutscher Wetterdienst, Offenbach/Main.

Marquard E., Weigelt A., Temperton V. M., Roscher C., Schumacher J., Buchmann N., Fischer M., Weisser W. W. & Schmid B. (2009). Plant species richness and functional composition drive overyielding in a 6-year grassland experiment. *Ecology*, **in press**.

Marquard E., Schmid B. & Weigelt A. (in preparation). Contrasting species performance in monoculture and mixture explains temporal changes in biodiversity effects.

Oelmann Y., Kreutziger Y., Temperton V. M., Buchmann N., Roscher C., Schumacher J., Schulze E. D., Weisser W. W. & Wilcke W. (2007a). Nitrogen and phosphorus budgets in experimental grasslands of variable diversity. *Journal of Environmental Quality*, **36**, 396-407.

Oelmann Y., Wilcke W., Temperton V. M., Buchmann N., Roscher C., Schumacher J., Schulze E. D. & Weisser W. W. (2007b). Soil and plant nitrogen pools as related to plant diversity in an experimental grassland. *Soil Science Society of America Journal*, **71**, 720-729.

Petermann J. S., Fergus A. J. F., Roscher C., Turnbull L. A., Weigelt A. & Schmid B. (2009). Biology, chance or history? The predictable re-assembly of temperate grassland communities. *Ecology*, accepted.

Roscher C., Schumacher J., Baade J., Wilcke W., Gleixner G., Weisser W. W., Schmid B. & Schulze E.-D. (2004). The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. *Basic and Applied Ecology*, **5**, 107-121.

Roscher C., Temperton V. M., Scherer-Lorenzen M., Schmitz M., Schumacher J., Schmid B., Buchmann N., Weisser W. W. & Schulze E.-D. (2005). Overyielding in experimental grassland communities - irrespective of species pool or spatial scale. *Ecology Letters*, **8**, 419-429.

Roscher C., Beßler H., Oelmann Y., Engels C., Wilcke W. & Schulze E.-D. (2009a). Resources, recruitment limitation and invader species identity determine pattern of spontaneous invasion in experimental grasslands. *Journal of Ecology*, **97**, 32-47.

Roscher C., Temperton V. M., Buchmann N. & Schulze E.-D. (2009b). Community assembly and biomass production in regularly and never weeded experimental grasslands. *Acta Oecologia*, **35**, 206-217.

Scherber C., Mwangi P. N., Temperton V. M., Roscher C., Schumacher J., Schmid B. & Weisser W. W. (2006). Effects of plant diversity on invertebrate herbivory in experimental grassland. *Oecologia*, **147**, 489-500.

Schumacher J. & Roscher C. (2009). Differential effects of functional traits on aboveground biomass in semi-natural grasslands. *Oikos*, accepted.

Weigelt A., Schumacher J., Roscher C. & Schmid B. (2008). Does biodiversity increase spatial stability in plant community biomass? *Ecology Letters*, **11**, 338-347.

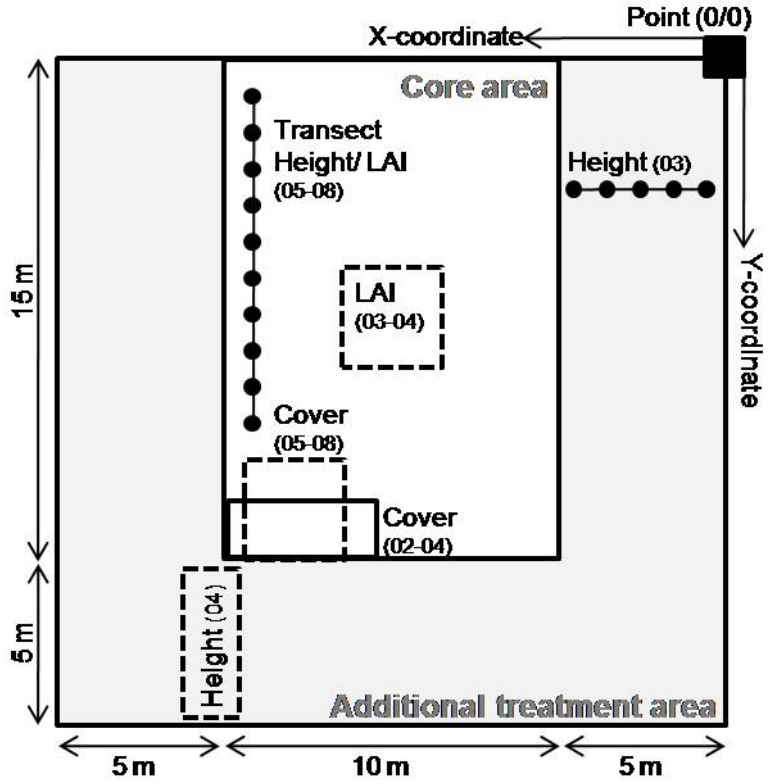

Fig. 1. Subdivision of experimental plots in the Jena-Experiment.

Chapter 4

Positive biodiversity–productivity relationship due to increased plant density

Elisabeth Marquard, Alexandra Weigelt, Christiane Roscher, Marlén Gubsch, Annett Lipowsky & Bernhard Schmid (2009) *Journal of Ecology*, doi: 10.1111/j.1365-2745.2009.01521.x..

Abstract

1. Positive effects of biodiversity on plant productivity may result from diversity-induced changes in the size or density of individual plants, yet these two possibilities have never been tested at the same time in a biodiversity experiment with a large species pool. Here, we distinguish between size effects and density effects on plant productivity, using data from 198 experimental grassland communities that contained 1–16 species. Plant modules such as tillers or rosettes were defined as relevant units, being equivalent to plant individuals in the majority of species.

2. In agreement with previous studies, we found positive effects of species richness on above-ground productivity. We show that this positive biodiversity effect resulted from diversity-induced increases in module density rather than from increases in module size. In contrast, variation in productivity within diversity levels was related to module size rather than module density.

3. The size–density relationships varied among plant functional groups and among-species but the average response to increasing species richness paralleled the pattern observed at the level of the entire plant communities: species richness had a positive effect on above-ground species biomass and species module density but not on species module size. Twenty-four out of 26 overyielding species had denser populations and 25 out of 28 underyielding species had smaller modules in mixtures than in monocultures.

4. ***Synthesis.*** In grasslands, an increase in community productivity must involve an increase in plant size or density. We found that diversity-induced increases in productivity were related to diversity-induced increases in density, whereas diversity-independent increases in productivity were related to increases in plant size. Our results suggest that increased density of overyielding species in mixtures was the main driver of the positive biodiversity–productivity relationship in our experiment. We conclude that the mechanisms leading to enhanced productivity of species-rich as compared with species-poor communities cannot be derived from mechanisms explaining high productivity within communities that contain a particular number of species.

Keywords: biodiversity–productivity relationships, ecosystem functioning, Jena Experiment, overyielding, plant modules, size–density relationships, species richness

Introduction

Evidence for a positive relationship between plant diversity and above-ground plant biomass production is accumulating for artificially assembled plant communities (Balvanera *et al.* 2006; Cardinale *et al.* 2006) as well as for natural ecosystems (Flombaum & Sala 2008; Tylianakis *et al.* 2008). Research on the mechanisms underlying positive biodiversity effects has mainly focused on separating effects of niche partitioning or facilitation (complementarity effects) from disproportionate effects of single species (selection effects, Loreau & Hector 2001; Tilman *et al.* 2001; Roscher *et al.* 2005; Fargione *et al.* 2007; Marquard *et al.* 2009). Irrespective of whether complementarity or selection effects enhance above-ground plant biomass in species-rich communities, the mechanism must involve an increase in the size or the number of plants.

Size–density–yield relationships are a central topic in plant population biology (Harper 1977). They form the basis of our understanding of self-regulation processes in plant populations. For example, they underlie the fundamental population biological principles of constant yield (Kira *et al.* 1953) and self-thinning (Yoda *et al.* 1963). In addition, the relationship between plant size and density within a population may strongly affect mortality and reproduction and may therefore have further consequences for the genetic diversity within the population as well as for community composition (Van Kleunen *et al.* 2005). However, size–density–yield relationships have rarely been investigated in plant mixtures (but see Bazzaz & Harper 1976; Schmid & Harper 1985; He *et al.* 2005; Roscher *et al.* 2007) and we still do not understand how they contribute to positive plant diversity–productivity relationships.

Varying the number of species within a plant community involves significant changes in the conditions experienced by individual plants. As species richness increases, intra-specific interactions among plants are replaced by inter-specific interactions and this may lead to a greater proportional light-, water- and nutrient availability for species that are complementary in their resource use (Naeem *et al.* 1994; Tilman *et al.* 1997b; Yachi & Loreau 2007) or to a reduced load of specialized pathogens per individual plant (Petermann *et al.* 2008). A species may respond to such changes in the available niche space by increasing plant size without a compensatory decrease in density or vice versa. In contrast, if niche space remains constant, any increase in size or density should be compensated for by a decrease in the other variable, as known from the law of constant yield in plant monocultures (Kira *et al.* 1953). Thus, if average overlap of resource or pathogen-niches among individual plants decreases with increasing species richness, different size–density relationships should be

observed between and within species richness levels. A diversity-induced increase in density or size without a compensatory reduction in the other variable could thus lead to a positive plant diversity–productivity relationship.

Previous studies concerning the biodiversity–productivity relationship found that in many species, individual plant biomass remained unchanged or even declined as species richness increased (Van Ruijven & Berendse 2003; Mwangi *et al.* 2007; Roscher *et al.* 2007). Given that in these studies sowing density was controlled and supposed to result in constant seedling densities across the diversity gradients, these results were unexpected. Here, we suggest that they were due to diversity-mediated changes in plant densities during the course of the experiments, e.g. differential seedling mortality or differential vegetative and sexual reproduction between species-rich and species-poor communities. We assessed both, plant densities and average plant size (calculated from total species biomass and density), for each species in a large-scale biodiversity experiment (Jena Experiment) to test the hypothesis that increased plant density rather than size leads to positive diversity–productivity relationships in plant communities.

The plant communities of the Jena Experiment represent temperate grasslands in which many plant species grow clonally and produce individual units which we refer to as modules (as opposed to genets which include all products of a single zygote, Harper & White 1974; Kays & Harper 1974; Harper 1977). More precisely, modules can be defined as demographic plant units with a high functional independence (e.g. tillers, shoots or rosettes, Schmid 1990). We assessed the effects of plant species richness on the three interrelated variables above-ground plant biomass, number of plant modules (= module density) and their individual biomass (= module size). Above-ground plant biomass, module density and module size were determined for the entire plant community (community level) as well as for the populations of the individual species present in the communities (species level). Furthermore, we investigated the effect of functional composition on these three variables because past research has shown that this component of diversity can be an important driver of above-ground biodiversity effects (Hooper & Vitousek 1997; Marquard *et al.* 2009).

We asked the following questions: (1) What is the effect of species richness and functional group composition on above-ground biomass, module density and module size at the level of entire plant communities? (2) What is the effect of species richness, functional group identity and species identity on above-ground biomass, module density and module size at the level of populations of individual species? (3) Does the relationship between above-ground biomass, module density and module size differ between and within species richness

levels? (4) Is an enhanced above-ground biomass production in mixtures related to changes in module density or module size with increasing species richness?

We show that in the studied grassland communities, diversity-induced increases in above-ground plant community biomass were predominantly caused by diversity-induced increases in module density. In contrast, increases in above-ground community biomass within richness levels were related to an increase in module size.

Methods

STUDY AREA AND EXPERIMENTAL DESIGN

The Jena Experiment is a large-scale biodiversity experiment situated in the floodplain of the river Saale near Jena (Germany, 50°55' N, 11°35' E, 130 m a.s.l.). Mean annual air temperature around Jena is 9.3 °C, and mean annual precipitation amounts to 587 mm (Kluge & Müller-Westermeier 2000). The topsoil of the 10-ha field site consists of sandy loam in the vicinity of the river, changing to silty clay with increasing distance from the river.

In May 2002, 78 experimental plant communities were established from seeds on plots of 20 x 20 m. Species compositions were determined by constrained random selection from a pool of 60 common Central European grassland species. Based on a cluster analysis of ecological and morphological traits, these 60 target species had been assigned to four functional groups: 16 grasses, 12 small herbs, 20 tall herbs and 12 legumes (Roscher *et al.* 2004). All possible combinations of species richness levels (1, 2, 4, 8 or 16 species) and functional group richness levels (1, 2, 3 or 4 functional groups) were sown, resulting in a near-orthogonal design of the experiment.

In addition to the 78 large plots, two replicate monocultures of each of the 60 species were sown on smaller plots of 3.5 x 3.5 m. On all plots, 1000 germinable seeds per m² were sown. They were evenly divided among the species in mixtures (seed numbers were adjusted according to germination tests performed in the laboratory prior to sowing, see Roscher *et al.* (2004) for details). Following the typical mowing regime for hay meadows, plots were mown twice per year in early June and in early September. Non-target species ("weeds") occurring within target communities were weeded out by hand during biannual weeding campaigns (early in the growing season and after the first mowing). Herbicides were used where target species composition allowed their application (herbicides against dicots in pure grass communities and against grasses in pure herb communities). The field site was divided into four blocks, each containing four large plots of the species richness levels 1, 2, 4 and 8, three

or four 16-species mixtures and 30 monocultures of small plot size. Weeding, mowing and herbicide spraying were completed blockwise.

MODULE DEFINITIONS

Because many of our target species grew clonally and produced dense vegetation on most experimental plots, different plant genets were no longer distinguishable 4 years after sowing. Therefore, plant modules were defined as the relevant units. A module represented either a separate plant individual or a plant part that would potentially grow independently if separated from the rest of the genet (Harper & White 1974; Harper 1977; Schmid 1990). Depending on the growth form of the species, these units were mostly single tillers, shoots or rosettes (see Table S1 in Supporting Information for details). For species with creeping shoots we counted the number of nodes present on these shoots (e.g. in *Trifolium repens*, *Ajuga reptans*).

SAMPLING

In May 2006, we counted the number of plant modules per species (species module density) on all experimental plots (78 large plots and 120 small monocultures) in two rectangular subplots of 0.2 x 0.5 m. Community module density was calculated as the sum of species module densities per plot. On all large plots, we harvested the above-ground biomass within the subplots (above-ground community biomass) and separated it according to species (above-ground species biomass). Biomass samples were dried at 70 °C for at least 48 h. For all large plots, mean module size was calculated by dividing above-ground biomass by module density, at the level of the entire community (community module size) as well as at the level of species (species module size). Using mean values for "size" neglected the variation in size within the species and within the individual communities. However, measuring all or a selection of modules in our biomass samples individually would have taken too much time and was not necessary in order to test our hypothesis.

In the small monocultures, above-ground community biomass was not harvested. Instead, five or six plant modules were selected randomly and their dry mass was determined. Above-ground community biomass was then calculated by multiplying community module density with the mean size of these modules. Samples of *Anthriscus sylvestris*, *Bromus hordeaceus*, *Holcus lanatus*, *Pastinaca sativa* and *Primula veris* were not taken in 2006. For these five species, five or six plant modules were collected in May 2008, treated as described above and their dry mass was used to supplement the data set.

DATA ANALYSIS

We assessed the effects of species richness and functional group composition (presence of particular functional groups and their interactions) on above-ground community biomass, community module density and community module size using analysis of variance (ANOVA) with sequential sums of squares (Table 1, for effects of species richness see also Fig. 1). The data were log-transformed (base 10) in order to improve the normality of the error distribution. The term "functional group composition" was partitioned into a set of orthogonal contrasts for the main effects of the presence of each of the four functional groups and their 2- and 3-way interactions. The main effects of the four functional groups were fitted in decreasing order of the percentage of total variation explained by these functional groups if fitted first in the set of contrasts. We assessed the relationship between community module density and above-ground community biomass (Fig. 2a), between community module size and above-ground community biomass (Fig. 2d) and between community module density and community module size (Fig. 2g) by plotting these variables against each other on a log-log scale. To analyse how these relationships varied between species richness levels, we constructed a second series of graphs, using the means of the variables per species richness level (Fig. 2b,e,h). This removed the variation within the species richness levels and, therefore, a significant slope indicated a relationship between the corresponding variables due to variation between the species richness levels. To analyse how the above-mentioned relationships varied within species richness levels, we constructed a third series of graphs, using the residuals of simple linear regressions that included either above-ground community biomass, community module density or community module size as dependent variable and the natural logarithm of species richness as explanatory variable (Fig. 2c,f,i). Because deviations from the log-linear effect of species richness were small, the log-linear fit removed most of the variation among the species richness levels and, therefore, a significant slope indicated a relationship between the corresponding variables due to variation within the species richness levels. To infer the significance of the above-mentioned relationships we estimated the slope of the major axis regression line (MA-slope) and tested its significance by 10 000 random permutations using the Model-II program by Legendre (2001). Only significant MA-slopes are displayed with their P-value in the corresponding panels of Fig. 2.

We performed ANOVAs with sequential sums of squares to analyse how above-ground species biomass, species module size and species module density were affected by species richness, functional group identity and species identity (Table 2). As a caveat we note that these three analyses are interdependent because biomass is the product of size and

density. However, because our aim was to find out to which extent variation in biomass was paralleled by variation in size or density, it was essential to carry out all three analyses. To assess how species richness, functional group identity and species identity influenced the relationship between the two variables contributing to species biomass, i.e. species module density and species module size, we used an analysis of covariance in which the sums of products of these two variables were decomposed (Kempthorne 1969, p. 264–268, Table 3). For both types of analyses, ANOVA and analysis of covariance, the data were log-transformed (base 10) in order to improve the normality of the error distribution. Figure S1 illustrates the effect of species identity and functional group identity on the relationship between species module density and species module size. For all species-specific analyses (presented in Fig. S1 and Tables 2 and 3) above-ground species biomass and species module density were corrected for sowing proportions.

To improve the species' comparability we calculated the relative yield, relative size and relative density for 54 of our 60 target species. For the remaining six species this was impossible due to their very low abundance either in monoculture (*Campanula patula*, *Cardamine pratensis*, *Luzula campestris* and *Sanguisorba officinalis*) or in mixtures (*B. hordeaceus*, *Cynosurus cristatus*). The relative yield of a species (RY_i) is the quotient of the yield of a species in mixture (here: above-ground species biomass) and the yield of this species in monoculture (Trenbath 1974). Similarly, we calculated the relative size (RS_i) and relative density (RD_i) of a species as the quotient of its module size or module density in mixture and its module size or module density in monoculture, respectively. We then calculated the mean relative yield (RYI), mean relative size (RSI) and mean relative density (RDI) per species as follows:

$$RYI = 1/N_i * \sum (\log10 (RY_i * \text{species richness})),$$

$$RSI = 1/N_i * \sum (\log10 (RS_i)),$$

$$RDI = 1/N_i * \sum (\log10 (RD_i * \text{species richness})),$$

where N_i denotes the number of plots on which species i was present. We compared RYI, RSI and RDI to explore differences in biomass allocation to module size and module density between monocultures and mixtures among the different species (Fig. 3).

With the exception of the major axis regressions and permutation tests presented in Fig. 2 (performed with the Model-II program by Legendre (2001)), we used the statistical software R (Version 2.7.2, http://www.r-project.org) for all calculations and statistical analyses.

Results

As has been found in previous biodiversity experiments including the Jena Experiment, above-ground community biomass (log-transformed) increased with the logarithm of species richness in our experimental plant communities (Fig. 1a, Table 1) and was higher in plots containing legumes (614.4 g m^{-2} vs. 230.8 g m^{-2}, Table 1). The presences of the remaining three functional groups (main effects) did not affect above-ground community biomass.

Community module size (log-transformed) was not significantly affected by the logarithm of species richness (Fig. 1b, Table 1). However, plants had larger modules in plots containing legumes (0.85 g vs. 0.42 g) and smaller modules in plots containing grasses (0.33 g vs. 0.96 g, Table 1).

Community module density (log-transformed) increased with the logarithm of species richness (Fig. 1c, Table 1). Communities containing grasses were on average more than twice as dense as communities without grasses (2236 modules m^{-2} vs. 1032 modules m^{-2}); communities containing tall herbs produced on average 1426 modules m^{-2}, whereas communities without tall herbs produced 1907 modules m^{-2} (see corresponding effects in Table 1).

When we explored the interdependency between the three response variables above-ground community biomass, community module density and community module size, we found a positive relationship between community module density and above-ground community biomass (Fig. 2a) which largely resulted from an increase in both variables with increasing species richness (Figs 1a,c and 2b, Table 1). When the variation explained by species richness was removed from the total variation between the plots, the residual variation in above-ground community biomass was no longer positively correlated with the residual variation in community module density (Fig. 2c). This suggested that within a particular level of species richness, communities with a higher number of modules were not more productive than communities with fewer modules.

Furthermore, above-ground community biomass was positively related to community module size (Fig. 2d). However, community module size did not increase with increasing species richness (Figs 1b and 2e, Table 1). When the variation explained by species richness was removed from the total variation between the plots, the relationship between the residual variation in community module size and the residual variation in above-ground community biomass remained positive (Fig. 2f). Thus, while a larger module size did not drive the increase in above-ground community biomass between species richness levels, module size was determinant for the productivity within a particular level of species richness.

A trade-off between community module density and community module size existed among the plots (Fig. 2g). However, this trade-off did not exist between the different species richness levels (Fig. 2h). When the variation explained by species richness was removed from the total variation, the relationship between the residual variation in community module density and the residual variation in community module size remained significantly negative (Fig. 2i) with an MA-slope of –1.333. This value was more negative than the value of –1 expected according to the law of constant final yield (Kira *et al.* 1953), indicating the occurrence of thinning processes in communities within richness levels (expected slope of –3/2 or –4/3, Yoda *et al.* 1963; Enquist *et al.* 1998).

Averaged over all species, the logarithm of species richness had a positive effect on above-ground species biomass and species module density but not on species module size (Table 2). Furthermore, the identity of the species and the particular functional group to which it belonged influenced its biomass allocation to module size and module density (Fig. S1, Tables 2 and 3). Generally, the relationship between species module density and species module size was strongly negative among species (Fig. S1) and was not affected by species richness (Table 3). Tall herbs tended to produce large but few modules and grasses produced small but numerous modules. Legumes and small herbs varied considerably in size and numbers of modules (Fig. S1).

Ranking the species according to their RYI revealed that 26 species were on average more productive and 28 species less productive in mixtures than in monocultures (Fig. 3). Legumes were mostly among the overyielding species (RYI > 1) and grasses mostly among the underyielding species (RYI < 1). Furthermore, an RYI > 1 was nearly always linked to an RDI > 1 (24 out of 26 species) whereas an RYI < 1 was nearly always linked to an RSI < 1 (25 out of 28 species). This pattern indicated that most of the overyielding species produced denser populations in mixtures than in monocultures while underyielding species had nearly always smaller modules in mixtures than in monocultures. Some species were able to increase their density as well as their size in mixtures compared with monocultures (evident particularly for *Lathyrus pratensis*, *Trifolium repens*, *Rumex acetosa*, *Veronica chamaedrys*, *Galium mollugo*). However, an RDI ≤ 1 was rarely overcompensated by an increased module size to result in an RYI > 1 (except in *Poa pratensis* and *Plantago lanceolata*).

Discussion

Our results confirm that plant diversity–productivity relationships are usually positive, as it was found in a number of other studies (Naeem *et al.* 1994; Hector *et al.* 1999; Tilman *et al.*

2001; Hooper *et al.* 2005; Roscher *et al.* 2005; Balvanera *et al.* 2006; Cardinale *et al.* 2006; Van Ruijven & Berendse 2009). Legume presence was the most influential component of functional composition regarding above-ground community biomass and community module size. This result is in line with previous findings (Spehn *et al.* 2002; Hector *et al.* 2007) and may be explained by the improved nitrogen availability in the soil of legume-containing plots (Temperton *et al.* 2007). The negative effect of grasses on community module size as well as the positive effect of grasses and the negative effect of tall herbs on community module density may be explained by the different size–number relationships of these functional groups: grasses produced on average many small and tall herbs produced on average few large modules.

The positive effect of species richness on above-ground community biomass was mainly driven by a diversity-induced increase in the number of plant modules per area. Thus, communities became denser as species richness increased but the average size of plant modules remained constant. Some evidence for a positive effect of species richness on community module density has been reported previously (Kennedy *et al.* 2002; Mwangi 2006; Schmitz 2007), but could not directly be related to increased community biomass because density and biomass were not measured on the same sample and thus mean module size could not be calculated. In another study a positive effect of plant species richness on above-ground community biomass was mainly due to one particular species (the grass *Arrhenatherum elatius*) that increased its density as well as its size (Roscher *et al.* 2007; Lorentzen *et al.* 2008).

Here, we could show that only diversity-induced increases in community module density resulted in an increase in community biomass whereas diversity-independent increases in module density did not. The diversity-induced increase in density could have resulted from an increased availability of germination or establishment sites for the different species as intraspecific neighbours were replaced by interspecific ones, reducing overlap in resource or pathogen niches between neighbouring individuals (Mwangi *et al.* 2007; Petermann *et al.* 2008). A previous study in the Jena Experiment found that the establishment of individual plant genets was indeed enhanced in species-rich communities (Schmitz 2007). It is thus likely that this process also worked in our communities.

Within species richness levels, the lack of a positive relationship between community module density and community biomass indicated that an increase in community module density must have been balanced by a reduction in community module size and, here, community module density was indeed negatively related to community module size.

However, the log-log slope of this size–density relationship was more negative than –1. This was consistent with our finding that within species richness levels an increase in module size resulted in an increase in community biomass. Furthermore, the empirical value of –1.333 for the log-log slope of the size–density relationship within richness levels equalled exactly the slope –4/3 predicted by Enquist *et al.* (1998) for size–density relationships in resource-limited plant populations, and was close to the slope of –3/2 predicted by Yoda *et al.* (1963) for monocultures undergoing thinning. Therefore, thinning, i.e. density-dependent mortality, probably occurred among communities of the same species richness. We conclude that the effects of increased module density and possibly also its causes differed between and within species richness levels. Whereas communities of the same species richness seemed to follow the common thinning rules (He *et al.* 2005) these rules could not explain differences in productivity between communities of different species richness.

In contrast to the well studied size–density relationships in monocultures (Harper 1977), community-wide size–density relationships in mixtures may be determined by particular species while others diverge from the mean trend. Indeed, similar to the mixed responses of individual species to changes in species richness that were reported from previous experiments (Naeem *et al.* 1996; Tilman *et al.* 1997a; Hector *et al.* 1999; Troumbis *et al.* 2000; Hector *et al.* 2002; Van Ruijven & Berendse 2003; Dimitrakopoulos & Schmid 2004; Hooper & Dukes 2004; Roscher *et al.* 2007; Lorentzen *et al.* 2008), not all of our target species reacted in the same way to increasing species richness (Tables 2 and 3, Fig. 3). However, their average response confirmed the pattern observed at the level of entire plant communities (compare Table 1 with Table 2). Comparisons between the performance of species in monoculture and mixture revealed that about half of the species had on average a lower biomass in mixture than in monoculture (see Fig. 3). The nevertheless positive relationship between species richness and above-ground community biomass therefore resulted from compositional effects: with increasing species richness the sum of the absolute differences between monocultures and mixtures of the overyielding species must have been increasingly larger than the sum of the absolute differences between monocultures and mixtures of the underyielding species. Being a relative measure, the sum of relative yields of the individual species in a community (i.e. the relative yield total) does not reflect such overcompensation. We further conclude from our observation of positive as well as negative relative yields of individual species that the positive effect of species richness on above-ground community biomass was not exclusively caused by complementarity effects but in part by selection effects. A mixture of both these mechanisms has been found to operate in the

Jena Experiment also in other years (Marquard *et al.* 2009) and has been suggested to commonly underlie positive effects of plant diversity on plant community biomass (Cardinale *et al.* 2007).

In conclusion, we showed that in our experimental grassland communities diversity-induced increases in community module density explained the positive species richness–productivity relationship while positive effects of community module size on productivity were diversity-independent. Both measures, module size and module density, possibly change along with resource availability. However, changes in module density may also reflect differential success of germination or establishment as well as differential mortality with potential consequences for the genetic diversity within the plant communities and for community composition (Van Kleunen *et al.* 2005). Distinguishing between size effects and density effects may therefore help to elucidate further consequences of biodiversity effects.

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Chapter references

Balvanera P., Pfisterer A. B., Buchmann N., He J.-S., Nakashizuka T., Raffaelli D. & Schmid B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, **9**, 1-11.

Bazzaz F. A. & Harper J. L. (1976). Relationship between plant weight and numbers in mixed populations of Sinapsis alba (L.) Rabenh. and Lepidium sativum L. *Journal of Applied Ecology*, **13**, 211-216.

Cardinale B. J., Srivastava D. S., Duffy J. E., Wright J. P., Downing A. L., Sankaran M. & Jouseau C. (2006). Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, **443**, 989-992.

Cardinale B. J., Wrigh J. P., Cadotte M. W., Carroll I. T., Hector A., Srivastava D. S., Loreau M. & Weis J. J. (2007). Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences*, **104**, 18123-18128.

Dimitrakopoulos P. G. & Schmid B. (2004). Biodiversity effects increase linearly with biotope space. *Ecology Letters*, **7**, 574-583.

Enquist B. J., Brown J. H. & West G. B. (1998). Allometric scaling of plant energetics and population density. *Nature*, **395**, 163-165.

Fargione J., Tilman D., Dybzinski R., Hille Ris Lambers J., Clark C., Harpole W. S., Knops J. M. H., Reich P. B. & Loreau M. (2007). From selection to complementarity: shifts in the causes of biodiversity-productivity relationships in a long-term biodiversity experiment. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **274**, 871-876.

Flombaum P. & Sala O. E. (2008). Higher effect of plant species diversity on productivity in natural than artificial ecosystems. *Proceedings of the National Academy of Sciences*, **105**, 6087-6090.

Harper J. L. & White J. (1974). The demography of plants. *Annual Review of Ecology and Systematics*, **5**, 419-463.

Harper J. L. (1977). *Population biology of plants.* Academic Press, London, UK.

He J.-S., Wolfe-Bellin K. S., Schmid B. & Bazzaz F. A. (2005). Density may alter diversity-productivity relationships in experimental plant communities. *Basic and Applied Ecology*, **6**, 505-517.

Hector A., Schmid B., Beierkuhnlein C., Caldeira M. C., Diemer M., Dimitrakopoulos P. G., Finn J. A., Freitas H., Giller P. S., Good J., Harris R., Högberg P., Huss-Danell K., Joshi J., Jumpponen A., Körner C., Leadley P. W., Loreau M., Minns A., Mulder C. P. H., O'Donovan G., Otway S. J., Pereira J. S., Prinz A., Read D. J., Scherer-Lorenzen M., Schulze E.-D., Siamantziouras A.-S. D., Spehn E. M., Terry A. C., Troumbis A. Y., Woodward F. I., Yachi S. & Lawton J. H. (1999). Plant diversity and productivity experiments in European grasslands. *Science*, **286**, 1123-1127.

Hector A., Bazeley-White E., Loreau M., Otway S. & Schmid B. (2002). Overyielding in grassland communities: testing the sampling effect hypothesis with replicated biodiversity experiments. *Ecology Letters*, **5**, 502-511.

Hector A., Joshi J., Scherer-Lorenzen M., Schmid B., Spehn E. M., Wacker L., Weilenmann M., Bazeley-White E., Beierkuhnlein C., Caldeira M. C., Dimitrakopoulos P. G., Finn J. A., Huss-Danell K., Jumpponen A., Leadley P. W., Loreau M., Mulder C. P. H., Neßhöver C., Palmborg C., Read D. J., Siamantziouras A. S. D., Terry A. C. & Troumbis A. Y. (2007). Biodiversity and ecosystem functioning: reconciling the results of experimental and observational studies. *Functional Ecology*, **21**, 998-1002.

Hooper D. U. & Vitousek P. M. (1997). The effects of plant composition and diversity on ecosystem processes. *Science*, **277**, 1302-1305.

Hooper D. U. & Dukes J. S. (2004). Overyielding among plant functional groups in a long-term experiment. *Ecology Letters*, **7**, 95-105.

Hooper D. U., Chapin F. S., Ewel J. J., Hector A., Inchausti P., Lavorel S., Lawton J. H., Lodge D. M., Loreau M., Naeem S., Schmid B., Setälä H., Symstad A. J., Vandermeer J. & Wardle D. A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3-35.

Kays S. & Harper J. L. (1974). The regulation of plant and tiller density in a grass sward. *Journal of Ecology*, **62**, 97-105.

Kempthorne O. (1969). *An introduction to genetic statistics.* The Iowa State University Press, Ames.

Kennedy T. A., Naeem S., Howe K. M., Knops J. M. H., Tilman D. & Reich P. (2002). Biodiversity as a barrier to ecological invasion. *Nature*, **417**, 636-638.

Kira T., Ogawa H. & Shinozaki K. (1953). Intraspecific competition among higher plants. I. Competition-density-yield interrelationships in regularly dispersed populations. *Journal of the Polytechnic Institute, Osaka Citiy University, Series D*, **4**, 1-16.

Kluge G. & Müller-Westermeier G. (2000). *Das Klima ausgewählter Orte der Bundesrepublik Deutschland: Jena.* Deutscher Wetterdienst, Offenbach/Main.

Legendre P. (2001). Model II regression - User's guide. Département de sciences biologiques, Université de Montréal [WWW document]. http://www.fas.umontreal.ca/biol/legendre/.

Loreau M. & Hector A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, **412**, 72-76.

Lorentzen S., Roscher C., Schumacher J., Schulze E.-D. & Schmid B. (2008). Species richness and identity affect the use of aboveground space in experimental grasslands. *Perspectives in Plant Ecology Evolution and Systematics*, **10**, 73-87.

Marquard E., Weigelt A., Temperton V. M., Roscher C., Schumacher J., Buchmann N., Fischer M., Weisser W. W. & Schmid B. (2009). Plant species richness and functional composition drive overyielding in a 6-year grassland experiment. *Ecology*, **in press**.

Mwangi P. N. (2006). Using phytometers to study the effects of plant diversity on ecosystem functioning. PhD-Thesis. Mathematisch-naturwissenschaftliche Fakultät, University of Zürich, Zürich.

Mwangi P. N., Schmitz M., Scherber C., Roscher C., Schumacher J., Scherer-Lorenzen M., Weisser W. W. & Schmid B. (2007). Niche pre-emption increases with species richness in experimental plant communities. *Journal of Ecology*, **95**, 65-78.

Naeem S., Thompson L. J., Lawler S. P., Lawton J. H. & Woodfin R. M. (1994). Declining biodiversity can alter the performance of ecosystems. *Nature*, **368**, 734-737.

Naeem S., Hakansson K., Lawton J. H., Crawley M. J. & Thompson L. J. (1996). Biodiversity and plant productivity in a model assemblage of plant species. *Oikos*, **76**, 259-264.

Petermann J. S., Fergus A. J. F., Turnbull L. A. & Schmid B. (2008). Janzen-Connell effects are widespread and strong enough to maintain diversity in grasslands. *Ecology*, **89**, 2399-2406.

Roscher C., Schumacher J., Baade J., Wilcke W., Gleixner G., Weisser W. W., Schmid B. & Schulze E.-D. (2004). The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. *Basic and Applied Ecology*, **5**, 107-121.

Roscher C., Temperton V. M., Scherer-Lorenzen M., Schmitz M., Schumacher J., Schmid B., Buchmann N., Weisser W. W. & Schulze E.-D. (2005). Overyielding in experimental grassland communities - irrespective of species pool or spatial scale. *Ecology Letters*, **8**, 419-429.

Roscher C., Schumacher J., Weisser W. W., Schmid B. & Schulze E. D. (2007). Detecting the role of individual species for overyielding in experimental grassland communities composed of potentially dominant species. *Oecologia*, **154**, 535-549.

Schmid B. & Harper J. L. (1985). Clonal growth in grassland perennials. 1. Density and pattern-dependent competition between plants with different growth forms. *Journal of Ecology*, **73**, 793-808.

Schmid B. (1990). Some Ecological and Evolutionary Consequences of Modular Organization and Clonal Growth in Plants. *Evolutionary Trends in Plants*, **4**, 25-34.

Schmitz M. (2007). How plant population processes mediate biodiversity effects on ecosystem functioning. PhD-Thesis. Mathematisch-naturwissenschaftliche Fakultät, University of Zürich, Zürich.

Spehn E. M., Scherer-Lorenzen M., Schmid B., Hector A., Caldeira M. C., Dimitrakopoulos P. G., Finn J. A., Jumpponen A., O'Donnovan G., Pereira J. S., Schulze E. D., Troumbis A. Y. & Körner C. (2002). The role of legumes as a component of biodiversity in a cross-European study of grassland biomass nitrogen. *Oikos*, **98**, 205-218.

Temperton V. M., Mwangi P. N., Scherer-Lorenzen M., Schmid B. & Buchmann N. (2007). Positive interactions between nitrogen-fixing legumes and four different neighbouring species in a biodiversity experiment. *Oecologia*, **151**, 190-205.

Tilman D., Knops J., Wedin D., Reich P., Ritchie M. & Siemann E. (1997a). The influence of functional diversity and composition on ecosystem processes. *Science*, **277**, 1300-1302.

Tilman D., Lehman C. L. & Thomson K. T. (1997b). Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences*, **94**, 1857-1861.

Tilman D., Reich P. B., Knops J., Wedin D., Mielke T. & Lehman C. (2001). Diversity and productivity in a long-term grassland experiment. *Science*, **294**, 843-845.

Trenbath B. R. (1974). Biomass productivity of mixtures. *Advances in Agronomy*, **26**, 177-210.

Troumbis A. Y., Dimitrakopoulos P. G., Siamantziouras A. S. D. & Memtsas D. (2000). Hidden diversity and productivity patterns in mixed Mediterranean grasslands. *Oikos*, **90**, 549-559.

Tylianakis J. M., Rand T. A., Kahmen A., Klein A. M., Buchmann N., Perner J. & Tscharntke T. (2008). Resource heterogeneity moderates the biodiversity-function relationship in real world ecosystems. *Plos Biology*, **6**, 947-956.

Van Kleunen M., Fischer M. & Schmid B. (2005). Three generations under low versus high neighborhood density affect the life history of a clonal plant through differential selection and genetic drift. *Oikos*, **108**, 573-581.

Van Ruijven J. & Berendse F. (2003). Positive effects of plant species diversity on productivity in the absence of legumes. *Ecology Letters*, **6**, 170-175.

Van Ruijven J. & Berendse F. (2009). Long-term persistence of a positive plant diversity–productivity relationship in the absence of legumes. *Oikos*, **118**, 101-106.

Yachi S. & Loreau M. (2007). Does complementary resource use enhance ecosystem functioning? A model of light competition in plant communities. *Ecology Letters*, **10**, 54-62.

Yoda K., Kira T., Ogawa H. & Hozumi K. (1963). Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology, Osaka City University*, **14**, 107-129.

Table 1. Summary of ANOVAs for the logarithm of above-ground community biomass, the logarithm of community module size and the logarithm of community module density, using sequential sums of squares. Indented terms show orthogonal contrasts for the effects of the presence of particular functional groups (summarized as "Main FG effects") and their 2- and 3-way interactions (summarized as "FG interactions"). The sum of contrast terms corresponds to FG composition.

		Log (above-gr. community biomass)				**Log (community module size)**				**Log (community module density)**			
Source	**d.f.**	**SS**	**MS**	**F**	**P**	**SS**	**MS**	**F**	**P**	**SS**	**MS**	**F**	**P**
Block	3	0.24	0.08	0.87	0.465	1.16	0.39	1.61	0.198	1.83	0.61	4.70	**0.005**
Ln (species richness (SR))	1	2.85	2.85	30.88	**<0.001**	0.01	0.01	0.04	0.844	2.54	2.54	19.59	**<0.001**
FG composition	12	2.75	0.23	2.48	**0.011**	6.34	0.53	2.19	**0.025**	3.81	0.32	2.45	**0.012**
Main FG effects	4	1.73	0.43	4.69	**0.002**	4.72	1.18	4.89	**0.002**	3.46	0.87	6.68	**<0.001**
Presence legumes	1	1.42	1.42	15.34	**<0.001**	2.36	2.36	9.78	**0.003**	0.12	0.12	0.92	0.341
Presence grasses	1	0.03	0.03	0.29	0.592	1.47	1.47	6.10	**0.017**	1.90	1.90	14.64	**<0.001**
Presence small herbs	1	0.22	0.22	2.36	0.130	0.06	0.06	0.23	0.630	0.05	0.05	0.42	0.522
Presence tall herbs	1	0.07	0.07	0.76	0.387	0.83	0.83	3.45	0.069	1.39	1.39	10.73	**0.002**
FG interactions*	8	1.02	0.13	1.38	0.225	1.62	0.20	0.84	0.570	0.34	0.04	0.33	0.950
Ln (SR) : FG composition	4	0.13	0.03	0.34	0.847	1.58	0.39	1.64	0.178	1.42	0.36	2.75	0.037
Residuals	*56*	*5.18*	*0.09*			*13.51*	*0.24*			*7.26*	*0.13*		

** includes: presence legumes x grasses, legumes x small herbs, legumes x tall herbs, grasses x small herbs, grasses x tall herbs, small herbs x tall herbs, legumes x grasses x small herbs and legumes x small herbs x tall herbs*

Table 2. Summary of ANOVAs for the logarithm of above-ground species biomass, the logarithm of species module size and the logarithm of species module density, using sequential sums of squares. The natural logarithm of species richness, species identity and the interaction between these terms were tested against the residuals. Functional group identity and the interaction between the natural logarithm of species richness and functional group identity were tested against species identity and the interaction between the natural logarithm of species richness and species identity, respectively. Above-ground species biomass and species module density were corrected for sowing proportions.

		Log (above-gr. species biomass)				**Log (species module size)**				**Log (species module density)**			
Source	**d.f.**	**SS**	**MS**	**F**	**P**	**SS**	**MS**	**F**	**P**	**SS**	**MS**	**F**	**P**
Ln (species richness (SR))	1	1.79	1.79	5.10	**0.025**	0.05	0.05	0.28	0.600	2.43	2.43	14.48	**<0.001**
Functional group (FG) identity	3	13.68	4.56	2.40	0.078	23.00	7.67	7.03	**<0.001**	13.15	4.38	2.81	**0.048**
Species identity	54	102.65	1.90	5.40	**<0.001**	58.90	1.09	6.27	**<0.001**	84.16	1.56	9.27	**<0.001**
Ln (SR) x FG identity	3	2.23	0.74	2.18	0.103	1.22	0.41	2.36	0.084	1.97	0.66	2.61	0.063
Ln (SR) x Species identity	46	15.69	0.34	0.97	0.535	7.90	0.17	0.99	0.500	11.57	0.25	1.50	**0.029**
Residuals	*217*	*76.37*	*0.35*			*37.83*	*0.17*			*36.55*	*0.17*		

Table 3. Summary of the analysis of covariance (Kempthorne, 1969, see "Methods") for the relationship between the logarithm of species module density and the logarithm of species module size, using sequential sums of products. The natural logarithm of species richness, species identity and the interaction between these terms were tested against the residuals. Functional group identity and the interaction between the natural logarithm of species richness and functional group identity were tested against species identity and the interaction between the natural logarithm of species richness and species identity, respectively. Species module density was corrected for sowing proportions. Abbreviations: d.f. cov.: degrees of freedom for covariance analysis, SP: sums of products, MSP: mean sums of products.

Source	d.f. cov.	SP	MSP	F	P
Ln (species richness (SR))	1	0.29	0.29	1.64	0.202
Functional group (FG) identity	3	-11.76	-3.92	5.47	**0.002**
Species identity	54	-38.72	-0.72	3.99	**<0.001**
Ln (SR) x FG identity	3	-0.74	-0.25	1.89	0.145
Ln (SR) x Species identity	46	-6.02	-0.13	0.73	0.900
Residuals	*216*	-38.79	-0.18		

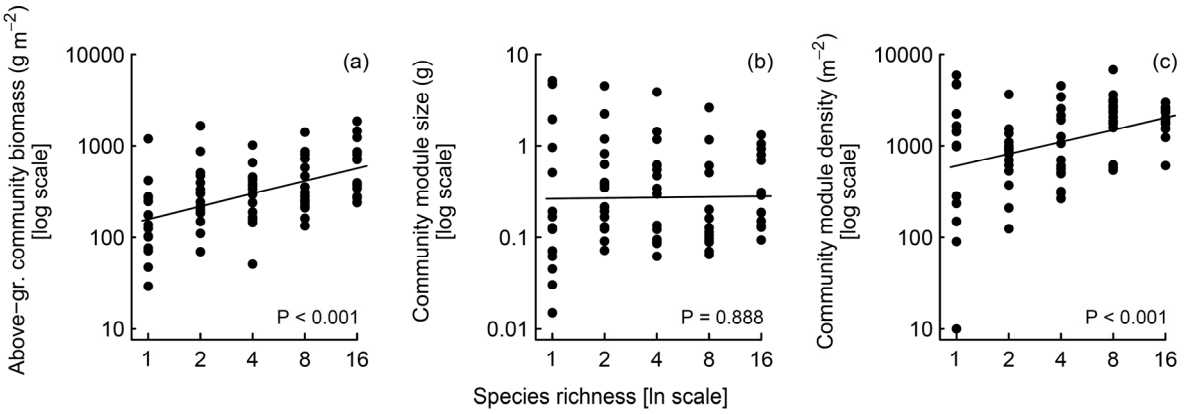

Fig. 1. Above-ground community biomass (a), community module size (b) and community module density (c) as a function of the natural logarithm of species richness. Data were log-transformed. Regression lines and the significance of their slopes (P) were obtained using linear models that contained the variable shown on the y-axis as dependent variable and the natural logarithm of species richness as explanatory variable.

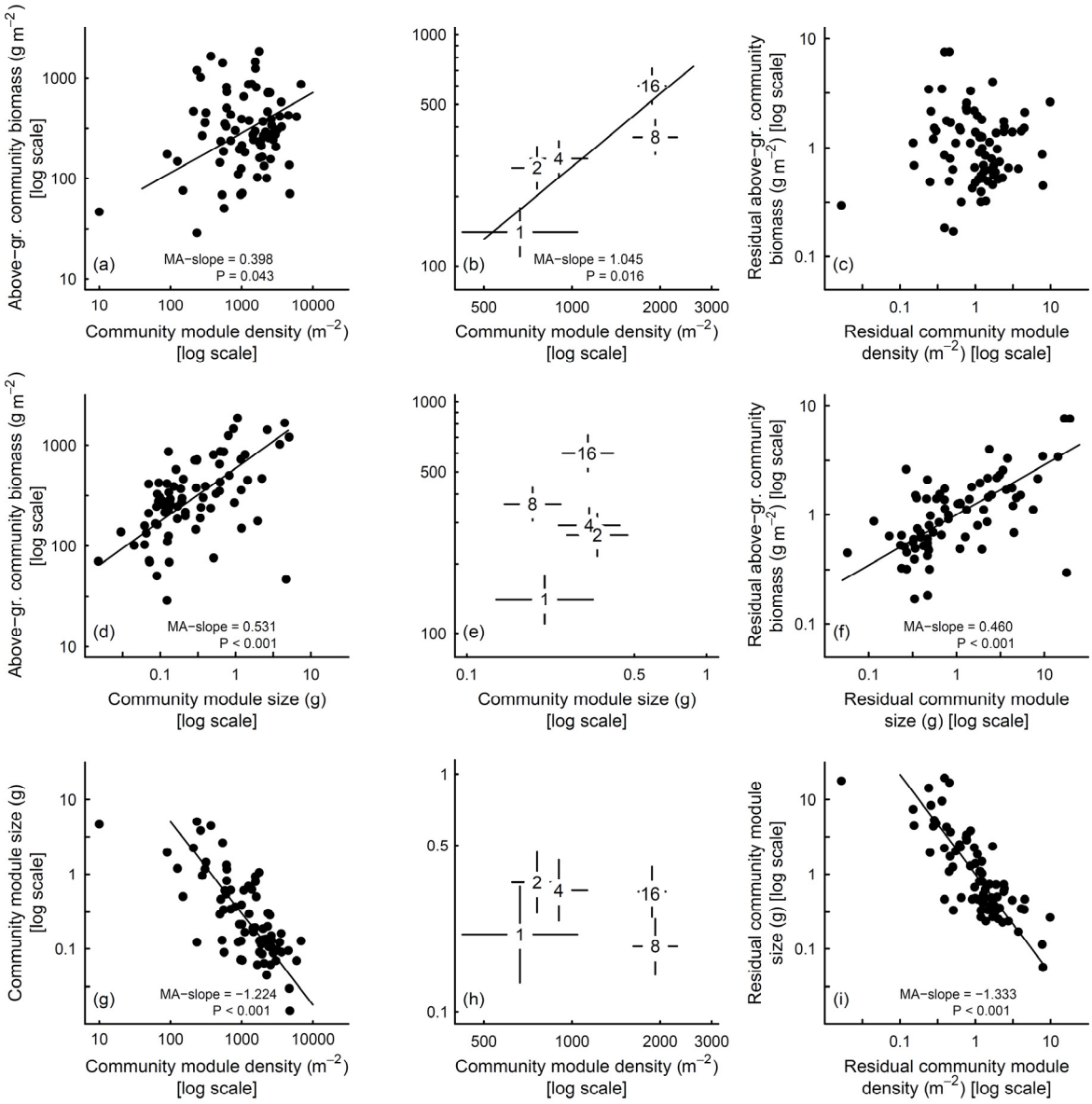

Fig. 2. Relationship between community module density and above-ground community biomass (a), community module size and above-ground community biomass (d) and community module density and community module size (g). (b), (e) and (h) show the respective relationships among the means ± 1 SE of the different species richness levels. (c), (f) and (i) show the relationship between the residuals of models that contained the variables shown in (b), (e) or (h), respectively, as dependent variable and the natural logarithm of species richness as explanatory variable. Data were log-transformed. A regression line was fitted by major axis regression (see "Methods") if a permutation test revealed that its slope was significantly different from 0 (indicated by $P < 0.05$).

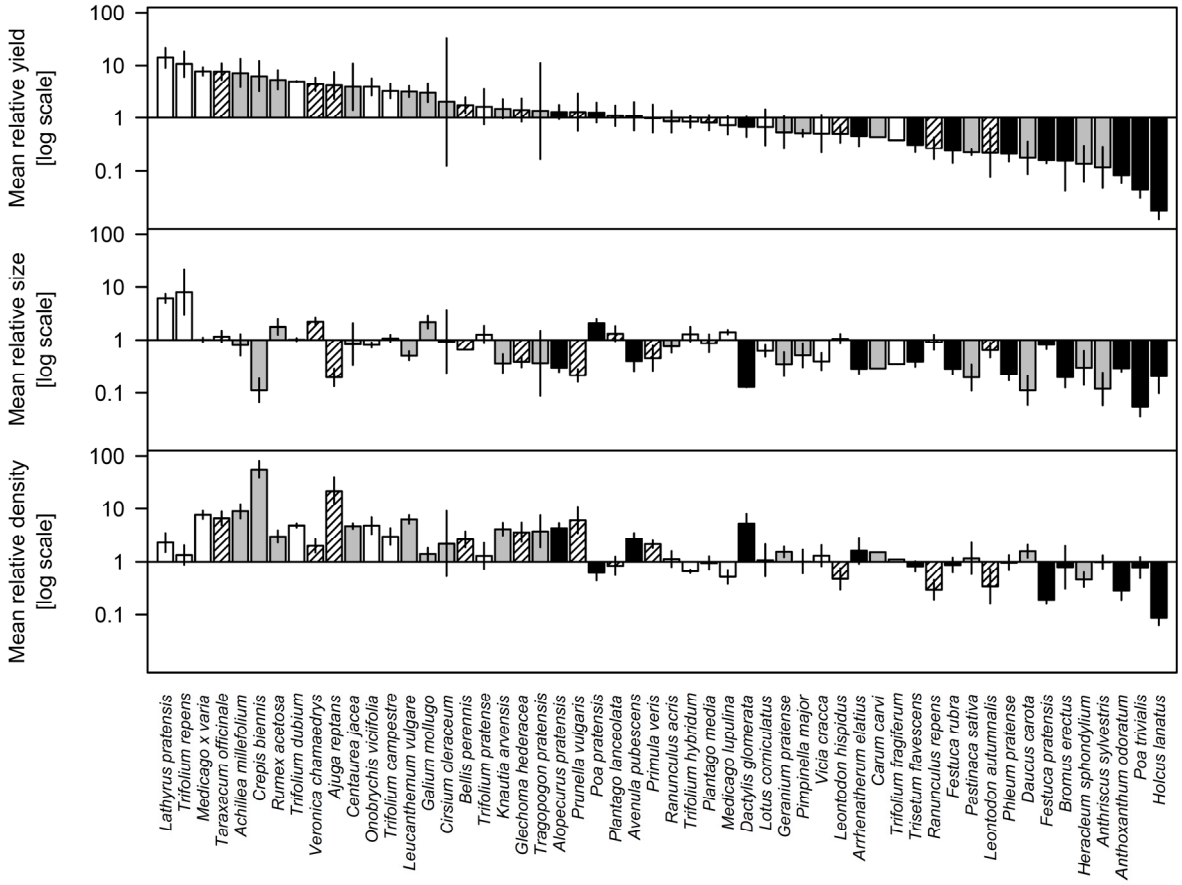

Fig. 3. Mean relative yield, mean relative size and mean relative density ± 1 SE for 54 species in the order of decreasing relative yield (see "Methods" for corresponding equations). Data were log-transformed prior to averaging. The different shading indicates the functional group identity of the species (blank: legumes, hatched: small herbs, grey: tall herbs, black: grasses).

Supporting information

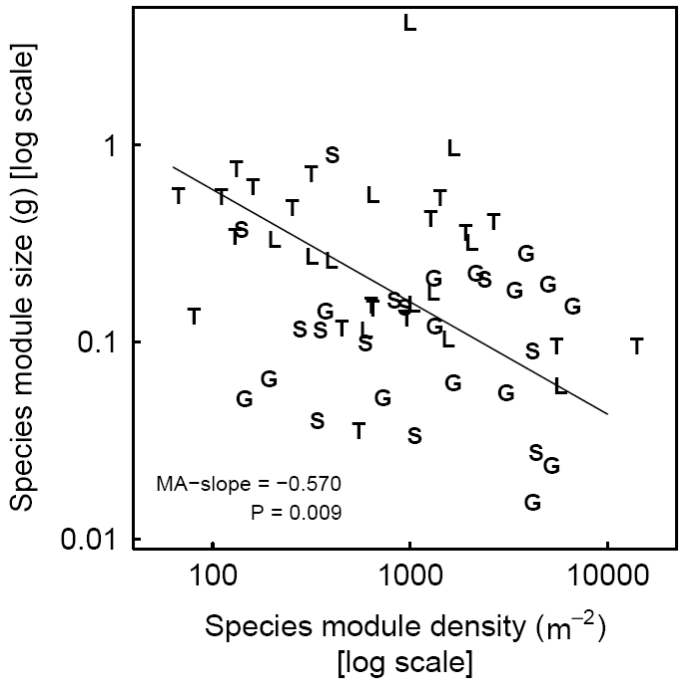

Fig. S1. Relationship between species module density and species module size. Data were log-transformed. Symbols indicate functional group identity of species (G = grass, S = small herb, T = tall herb, L = legume species). No values for *Bromus hordeaceus* and *Cardamine pratensis* due to their low abundance. The regression line was fitted by major axis regression (see "Methods") and the significance of its slope was tested by permutation.

Table S1. Module definition per species

Species	Unit defined as 1 module
Achillea millefolium	Rosette
Ajuga reptans	Rosette / node on horizontal shoot (with leaves)
Alopecurus pratensis	Tiller
Anthoxanthum odoratum	Tiller
Anthriscus sylvestris	Rosette / shoot*
Arrhenatherum elatius	Tiller
Avenula pubescens	Tiller
Bellis perennis	Rosette
Bromus erectus	Tiller
Bromus hordeaceus	Tiller
Campanula patula	Rosette / shoot*
Carum carvi	Rosette / shoot*
Cardamine pratensis	Rosette / shoot*
Centaurea jacea	Rosette / shoot*
Cirsium oleraceum	Rosette
Crepis biennis	Rosette / shoot*
Cynosurus cristatus	Tiller
Dactylis glomerata	Tiller
Daucus carota	Rosette / shoot*
Festuca pratensis	Tiller
Festuca rubra	Tiller
Galium mollugo	Shoot
Geranium pratense	Rosette / shoot*
Glechoma hederacea	Node on horizontal shoot (2 leaves = 1 module)
Heracleum sphondylium	Rosette / shoot*
Holcus lanatus	Tiller
Knautia arvensis	Rosette
Lathyrus pratensis	Shoot
Leontodon autumnalis	Rosette
Leontodon hispidus	Rosette
Leucanthemum vulgare	Rosette / shoot*
Lotus corniculatus	Shoot
Luzula campestris	Tiller
Medicago lupulina	Shoot
Medicago x varia	Shoot
Onobrychis viciifolia	Shoot
Pastinaca sativa	Rosette / shoot*
Phleum pratense	Tiller
Pimpinella major	Rosette / shoot*

Plantago lanceolata	Rosette
Plantago media	Rosette
Poa pratensis	Tiller
Poa trivialis	Tiller
Primula veris	Rosette
Prunella vulgaris	Vertical shoot (with roots)
Ranunculus acris	Rosette / shoot*
Ranunculus repens	Rosette / node on horizontal shoot (with leaves)
Rumex acetosa	Rosette
Sanguisorba officinalis	Shoot (leaves if singular)
Taraxacum officinale	Rosette
Tragopogon pratensis	Rosette / shoot*
Trifolium campestre	Shoot
Trifolium dubium	Shoot
Trisetum flavescens	Tiller
Trifolium fragiferum	Shoot
Trifolium hybridum	Shoot
Trifolium pratense	Shoot
Trifolium repens	Node (1 leave = 1 module)
Veronica chamaedrys	Vertical shoot (with roots)
Vicia cracca	Shoot

* Rosettes if no flower initiation, shoots if flower initiation.

General Discussion

In this thesis, I explored biodiversity–productivity relationships in manipulated grassland communities. I assessed the effects of species richness on aboveground community biomass and distinguished them from the effects of functional diversity (chapters 1 and 4). In particular, I analyzed whether increased biomass production in mixtures depended strongly on the presence of particular functional groups (chapters 1, 2 and 4) or species (chapter 2). I examined how the performance of species in mixtures corresponded to their performance in monocultures (chapters 1, 2 and 4) and, finally, how changes in plant size and plant density influenced community biomass production (chapter 4). All these analyses aimed at improving our comprehension of the mechanisms underlying positive biodiversity–productivity relationships.

In summary, I observed that species richness and functional composition were important drivers of the positive biodiversity–productivity relationship in the Jena Experiment. Increased species richness had a greater potential to enhance community biomass if the species belonged to different rather than the same functional groups (chapter 1). This was consistent with my observation that multifunctional communities were able to transgressively overyield plant assemblages containing a single functional group (chapter 1). However, biomass increases were not exclusively due to the addition of functionally different species. Instead, my results suggested that increasing the number of species within a community may lead to an increase in its biomass even if the added species belongs to a functional group already present in the community (chapter 1). This supported the conclusion derived from earlier experiments (Reich *et al.* 2004; Lanta & Lepš 2007) that species belonging to a particular functional group are not necessarily redundant in their function.

Furthermore, I demonstrated that the temporal development of biomass production differed depending on whether a species experienced intraspecific or interspecific competition and I found evidence for a declining correlation between the performance of a species in mixture and monoculture over time (chapters 1 and 2). Thus, several results presented in this thesis strongly suggest that positive biodiversity–productivity relationships are to a large extent driven by multiple-species interactions. This overall conclusion is in line with the outcome of a recent meta-analysis about the impacts of plant diversity on biomass production (Cardinale *et al.* 2007) and contradicts the hypothesis that biological characteristics of the dominant plants rather than the number of species control ecosystem productivity (Aarssen 1997; Grime 1997; Wardle 2001; Cardinale *et al.* 2006).

A significant contribution for advancing the field of biodiversity–productivity research may result from the methodology applied in chapters 1, 2 and 4 of this thesis. In the context of

biodiversity research, replacement series at the level of functional groups, comparisons between temporal changes in observed vs. expected yields and analyses of size–density–yield relationships are highly innovative analytical tools. They did not only provide new insights into the little explored issues of transgressive overyielding between functional groups, the potential degradation of monocultures over time and the effect of diversity on size–density–relationships but may also inspire further studies on these subjects and may encourage the use of novel or unconventional tools for data analysis.

Further merits of the presented analyses (and data sets) become evident in the light of the harsh criticism that research focused on the biodiversity–productivity relationship has received. Major issues of concern have been the artificiality and immaturity of assembled plant communities and the possibility to create artefacts through an inappropriate experimental design (Givnish 1994; Aarssen 1997; Garnier *et al.* 1997; Huston 1997; Doak *et al.* 1998; Wardle 1998; Thompson *et al.* 2005). In the Jena Experiment, the large plot size and the long time scale reduce the artificiality of these created grassland plots. The time scale is important because it is assumed that in experimental grasslands, interactions between species develop and change over several years after the initial manipulation (Pacala & Tilman 2002; Guo *et al.* 2006; Van Ruijven & Berendse 2009). For a sound evaluation of the consequences of biodiversity loss, it is therefore essential to consider longer time spans and to assess the temporal dynamics in the observed effects. The presented analyses of a multiple-year data set (chapter 1 and 2) showed indeed that biodiversity effects may vary considerably over time. However, I observed consistently positive net biodiversity effects which clearly rejected the hypothesis of biodiversity effects being transient (Thompson *et al.* 2005). This finding is consistent with the relatively few studies that have assessed biodiversity effects in controlled experimental set-ups running for more than three years (Tilman *et al.* 2006b; Van Ruijven & Berendse 2009). The provision of a multiple-year data set (chapter 3) may initiate other valuable studies focused on how species richness and functional diversity affect plant community composition and structure over time.

Another subject of debate has been the adequate experimental design for biodiversity studies. Shortly after the results of the first modern biodiversity experiments had been published (Naeem *et al.* 1994; Tilman *et al.* 1996; Hector *et al.* 1999), they were criticized for not allowing a separation of the effects of particular species traits (e.g. nitrogen fixation by legumes) from effects of species interactions (Aarssen 1997; Huston 1997; Wardle 1998) or a rigid test of the occurrence of transgressive overyielding (Garnier *et al.* 1997). In the Jena Experiment, these issues were tackled by a careful combination of species richness levels with

different functional group compositions. Making use of this improved design, I could show that functional differences between species promoted the occurrence of positive biodiversity effects and that the presence of legumes explained in part but not completely why some experimental plots were more productive than others (chapter 1). Similar conclusions about the role of legumes have been previously reported (Hector *et al.* 2007) and biodiversity effects have been demonstrated to occur even in the absence of legumes (Van Ruijven & Berendse 2003, 2009). Moreover, I presented strong evidence for facilitation and demonstrated that transgressive overyielding occurred between all pairs of functional groups and across the entire 5-year observation period (chapter 1). This important finding contradicted once more the hypothesis that a species-rich polyculture tends to be no different from a monoculture of the single most productive species (Cardinale *et al.* 2006).

The fact that in the Jena Experiment all species growing in multi-species assemblages are also grown in monoculture under the same environmental conditions allowed the application of the additive partitioning method by Loreau & Hector (2001) which revealed that complementarity effects increased over time. This was in line with the results from other biodiversity experiments (Spehn *et al.* 2005; Van Ruijven & Berendse 2005; Fargione *et al.* 2007). Furthermore, I was able to detect differences in the temporal development between species growing in mixture and monoculture. These differences may have resulted from negative plant–soil feedbacks or a particularly strong attack of foliar pathogens in monocultures, as has been reported previously (Knops *et al.* 1999; Mitchell *et al.* 2003; Bonanomi *et al.* 2005; Bell *et al.* 2006; Casper & Castelli 2007). However, my results did not support the hypothesis that a degradation of monocultures largely explains why net biodiversity effects tend to increase over time (chapter 2). In addition, I was able to show that an increased density of overyielding species was the predominant driver of the positive biodiversity–productivity relationship in the experimental plant communities of the Jena Experiment (chapter 4).

Mechanisms of biodiversity–productivity relationships may be studied at different scales and in more or less detail. In this thesis, I restricted my analyses to processes and patterns at the community level with special focus on the role of multi-species interactions for community biomass production and to the effects of plant diversity on community structure (size/density). From these analyses, I cannot draw conclusions about particular processes of species interactions such as the complementary use of nitrogen, water, light or space, but several other recent publications elucidate such interspecific interactions (e.g. Roscher *et al.* 2008; Verheyen *et al.* 2008; von Felten & Schmid 2008; Wacker 2008; Fornara & Tilman

2009; Hautier *et al.* 2009; von Felten *et al.* 2009). However, revealing the specific mechanisms that are responsible for a positive relationship between plant diversity and productivity remains a challenge for future research.

In conclusion, this thesis presents several results regarding the long-standing controversy about the nature and relevance of biodiversity–productivity relationships. I was able to obtain these significant findings because the Jena Experiment overcomes some of the methodological difficulties often hampering previous work on this subject. However, the Jena Experiment has also its weaknesses. Its design is based on the categorical distinction of functional groups despite the fact that the advantages of continuous measures over group-based measures of diversity have been reported in several publications (Bengtsson 1998; Díaz & Cabido 2001; Hooper *et al.* 2002; Petchey & Gaston 2002, 2006; Ricotta & Marignani 2007). Furthermore, the large plot size results in an enormous management effort and its advantages of reduced edge effects and an increased research area is partly compromised by the high pressure of weeds invading the target communities.

Nevertheless, the results presented in this thesis provide strong evidence that multi-species rather than single species effects mainly generate positive biodiversity effects. This finding may be highly relevant with regard to the future functionality of ecosystems. If a positive biodiversity–productivity relationship was the result of good competitors becoming dominant in mixtures (combined with the increased probability of their presence in species-rich communities) then dominant species alone could ensure high biomass production (Lawler *et al.* 2002). But compelling evidence for multi-species interactions operating to increase the productivity of ecosystems suggests the opposite: that the loss of other than the most productive species may also result in a decline of biomass production. The relevance of these findings for nature conservation is controversial because conservation efforts are usually not targeted at high ecosystem productivity (Schwartz *et al.* 2000; Srivastava & Vellend 2005). However, other important functions such as nutrient leaching, water cycling or resistance to weed invasion may be linked to primary productivity. If these functions are to be conserved, it may be crucial to save as much of the remaining biodiversity as possible. Furthermore, it seems highly desirable to combine the benefits of high plant diversity e.g. for associated insects, with the agronomists' interest in high forage yields. Several recent studies indicate that managing high-diversity, low impact grasslands may be a way to reconcile the aims of conservationists and farmers (Tilman *et al.* 2006a; Bullock *et al.* 2007; Kirwan *et al.* 2007; Weigelt *et al.* 2009). Therefore, an improved understanding of the mechanisms that lead to a

positive relationship between biodiversity and productivity may be relevant for making decisions on the management of agro-ecosystems.

Chapter references

Aarssen L. W. (1997). High productivity in grassland ecosystems: effected by species diversity or productive species? *Oikos*, **80**, 183-184.

Bell T., Freckleton R. P. & Lewis O. T. (2006). Plant pathogens drive density-dependent seedling mortality in a tropical tree. *Ecology Letters*, **9**, 569-574.

Bengtsson J. (1998). Which species? What kind of diversity? Which ecosystem function? Some problems in studies of relations between biodiversity and ecosystem function. *Applied Soil Ecology*, **10**, 191-199.

Bonanomi G., Rietkerk M., Dekker S. C. & Mazzoleni S. (2005). Negative plant-soil feedback and positive species interaction in a herbaceous plant community. *Plant Ecology*, **181**, 269-278.

Bullock J. M., Pywell R. F. & Walker K. J. (2007). Long-term enhancement of agricultural production by restoration of biodiversity. *Journal of Applied Ecology*, **44**, 6-12.

Cardinale B. J., Srivastava D. S., Duffy J. E., Wright J. P., Downing A. L., Sankaran M. & Jouseau C. (2006). Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, **443**, 989-992.

Cardinale B. J., Wrigh J. P., Cadotte M. W., Carroll I. T., Hector A., Srivastava D. S., Loreau M. & Weis J. J. (2007). Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences*, **104**, 18123-18128.

Casper B. B. & Castelli J. P. (2007). Evaluating plant-soil feedback together with competition in a serpentine grassland. *Ecology Letters*, **10**, 394-400.

Díaz S. & Cabido M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, **16**, 646-655.

Doak D. F., Bigger D., Harding E. K., Marvier M. A., O'Malley R. E. & Thomson D. (1998). The statistical inevitability of stability-diversity relationships in community ecology. *American Naturalist*, **151**, 264-276.

Fargione J., Tilman D., Dybzinski R., Hille Ris Lambers J., Clark C., Harpole W. S., Knops J. M. H., Reich P. B. & Loreau M. (2007). From selection to complementarity: shifts in the causes of biodiversity-productivity relationships in a long-term biodiversity experiment. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **274**, 871-876.

Fornara D. A. & Tilman D. (2009). Ecological mechanisms associated with the positive diversity-productivity relationship in an N-limited grassland. *Ecology*, **90**, 408-418.

Garnier E., Navas M. L., Austin M. P., Lilley J. M. & Gifford R. M. (1997). A problem for biodiversity-productivity studies: how to compare the productivity of multispecific plant mixtures to that of monocultures? *Acta Oecologica*, **18**, 657-670.

Givnish T. J. (1994). Does diversity beget stability? *Nature*, **371**, 113-114.

Grime J. P. (1997). Biodiversity and ecosystem function: the debate deepens. *Science*, **277**, 1260-1261.

Guo Q. F., Shaffer T. & Buhl T. (2006). Community maturity, species saturation and the variant diversity-productivity relationships in grasslands. *Ecology Letters*, **9**, 1284-1292.

Hautier Y., Niklaus P. A. & Hector A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science*, **324**, 636-638.

Hector A., Schmid B., Beierkuhnlein C., Caldeira M. C., Diemer M., Dimitrakopoulos P. G., Finn J. A., Freitas H., Giller P. S., Good J., Harris R., Högberg P., Huss-Danell K., Joshi J., Jumpponen A., Körner C., Leadley P. W., Loreau M., Minns A., Mulder C. P. H., O'Donovan G., Otway S. J., Pereira J. S., Prinz A., Read D. J., Scherer-Lorenzen M., Schulze E.-D., Siamantziouras A.-S. D., Spehn E. M., Terry A. C., Troumbis A. Y., Woodward F. I., Yachi S. & Lawton J. H. (1999). Plant diversity and productivity experiments in European grasslands. *Science*, **286**, 1123-1127.

Hector A., Joshi J., Scherer-Lorenzen M., Schmid B., Spehn E. M., Wacker L., Weilenmann M., Bazeley-White E., Beierkuhnlein C., Caldeira M. C., Dimitrakopoulos P. G., Finn J. A., Huss-Danell K., Jumpponen A., Leadley P. W., Loreau M., Mulder C. P. H., Neßhöver C., Palmborg C., Read D. J., Siamantziouras A. S. D., Terry A. C. & Troumbis A. Y. (2007). Biodiversity and ecosystem functioning: reconciling the results of experimental and observational studies. *Functional Ecology*, **21**, 998-1002.

Hooper D. U., Solan M., Symstad A., Díaz S., Gessner M. O., Buchmann N., Degrange V., Grime P., Hulot F., Mermillod-Blondin F., Roy J., Spehn E. & Van Peer L. (2002). Species diversity, functional diversity, and ecosystem functioning. In: *Biodiversity and ecosystem functioning: Synthesis and Perspectives* (eds. Loreau M., Naeem S. & Inchausti P.). Oxford University Press New York, pp. 195-208.

Huston M. A. (1997). Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, **110**, 449-460.

Kirwan L., Lüscher A., Sebastia M. T., Finn J. A., Collins R. P., Porqueddu C., Helgadottir A., Baadshaug O. H., Brophy C., Coran C., Dalmannsdottir S., Delgado I., Elgersma A., Fothergill M., Frankow-Lindberg B. E., Golinski P., Grieu P., Gustavsson A. M., Hoglind M., Huguenin-Elie O., Iliadis C., Jorgensen M., Kadziuliene Z., Karyotis T., Lunnan T., Malengier M., Maltoni S., Meyer V., Nyfeler D., Nykanen-Kurki P., Parente J., Smit H. J., Thumm U. & Connolly J. (2007). Evenness drives consistent diversity effects in intensive grassland systems across 28 European sites. *Journal of Ecology*, **95**, 530-539.

Knops J. M. H., Tilman D., Haddad N. M., Naeem S., Mitchell C. E., Haarstad J., Ritchie M. E., Howe K. M., Reich P. B., Siemann E. & Groth J. (1999). Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters*, **2**, 286-293.

Lanta V. & Lepš J. (2007). Effects of species and functional group richness on production in two fertility environments: an experiment with communities of perennial plants. *Acta Oecologica*, **32**, 93-103.

Lawler S. P., Armesto J. J. & Kareiva P. (2002). How relevant to conservation are studies linking biodiversity and ecosystem functioning? In: *Functional consequences of biodiversity: Experimental progress and theoretical extensions* (eds. Kinzig A., Tilman D. & Pacala P.). Princeton University Press Princeton, New Jersey, pp. 294-313.

Loreau M. & Hector A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, **412**, 72-76.

Mitchell C. E., Reich P. B., Tilman D. & Groth J. V. (2003). Effects of elevated CO2, nitrogen deposition, and decreased species diversity on foliar fungal plant disease. *Global Change Biology*, **9**, 438-451.

Naeem S., Thompson L. J., Lawler S. P., Lawton J. H. & Woodfin R. M. (1994). Declining biodiversity can alter the performance of ecosystems. *Nature*, **368**, 734-737.

Pacala P. & Tilman D. (2002). The transition from sampling to complementarity. In: *Functional consequences of biodiversity: Experimental progress and theoretical extensions* (eds. Kinzig A., Tilman D. & Pacala P.). Princeton University Press Princeton, New Jersey, pp. 151-166.

Petchey O. L. & Gaston K. J. (2002). Extinction and the loss of functional diversity. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **269**, 1721-1727.

Petchey O. L. & Gaston K. J. (2006). Functional diversity: back to basics and looking forward. *Ecology Letters*, **9**, 741-758.

Reich P. B., Tilman D., Naeem S., Ellsworth D. S., Knops J., Craine J., Wedin D. & Trost J. (2004). Species and functional group diversity independently influence biomass accumulation and its response to CO_2 and N. *Proceedings of the National Academy of Sciences*, **101**, 10101-10106.

Ricotta C. & Marignani M. (2007). Computing beta-diversity with Rao's quadratic entropy: a change of perspective. *Diversity and Distributions*, **13**, 237-241.

Roscher C., Thein S., Schmid B. & Scherer-Lorenzen M. (2008). Complementary nitrogen use among potentially dominant species in a biodiversity experiment varies between two years. *Journal of Ecology*, **96**, 477-488.

Schwartz M. W., Brigham C. A., Hoeksema J. D., Lyons K. G., Mills M. H. & Van Mantgem P. J. (2000). Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia*, **122**, 297-305.

Spehn E. M., Hector A., Joshi J., Scherer-Lorenzen M., Schmid B., Bazeley-White E., Beierkuhnlein C., Caldeira M. C., Diemer M., Dimitrakopoulos P. G., Finn J. A., Freitas H., Giller P. S., Good J., Harris R., Högberg P., Huss-Danell K., Jumpponen A., Koricheva J., Leadley P. W., Loreau M., Minns A., Mulder C. P. H., O'Donovan G., Otway S. J., Palmborg C., Pereira J. S., Pfisterer A. B., Prinz A., Read D. J., Schulze E.-D., Siamantziouras A.-S. D., Terry A. C., Troumbis A. Y., Woodward F. I., Yachi S. & Lawton J. H. (2005). Ecosystem effects of biodiversity manipulations in European grasslands. *Ecological Monographs*, **75**, 37-63.

Srivastava D. S. & Vellend M. (2005). Biodiversity-ecosystem function research: is it relevant to conservation? *Annual Review of Ecology, Evolution, and Systematics*, **36**, 267-294.

Thompson K., Askew A. P., Grime J. P., Dunnett N. P. & Willis A. J. (2005). Biodiversity, ecosystem fuction and plant traits in mature and immature plant communities. *Functional Ecology*, **19**, 355-358.

Tilman D., Wedin D. & Knops J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, **379**, 718-720.

Tilman D., Hill J. & Lehman C. (2006a). Carbon-negative biofuels from low-input high-diversity grassland biomass. *Science*, **314**, 1598-1600.

Tilman D., Reich P. B. & Knops J. M. (2006b). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, **441**, 629-632.

Van Ruijven J. & Berendse F. (2003). Positive effects of plant species diversity on productivity in the absence of legumes. *Ecology Letters*, **6**, 170-175.

Van Ruijven J. & Berendse F. (2005). Diversity-productivity relationships: initial effects, long-term patterns, and underlying mechanisms. *Proceedings of the National Academy of Sciences*, **102**, 695-700.

Van Ruijven J. & Berendse F. (2009). Long-term persistence of a positive plant diversity–productivity relationship in the absence of legumes. *Oikos*, **118**, 101-106.

Verheyen K., Bulteel H., Palmborg C., Olivie B., Nijs I., Raes D. & Muys B. (2008). Can complementarity in water use help to explain diversity-productivity relationships in experimental grassland plots? *Oecologia*, **156**, 351-361.

von Felten S. & Schmid B. (2008). Complementarity among species in horizontal versus vertical rooting space. *Journal of Plant Ecology*, **1**, 33-41.

von Felten S., Hector A., Buchmann N., Niklaus P., A., Schmid B. & Scherer-Lorenzen M. (2009). Belowground nitrogen partitioning in experimental grassland plant communities of varying species richness. *Ecology*, **90**, 1389-1399.

Wacker L. (2008). Diversity effects in early- and mid-successional experimental grasslands. PhD-Thesis. Mathematisch-naturwissenschaftliche Fakultät, University of Zürich, Zürich.

Wardle D. A. (1998). A more reliable design for biodiversity study? *Nature*, **394**, 30-30.

Wardle D. A. (2001). Experimental demonstration that plant diversity reduces invasibility - evidence of a biological mechanism or a consequence of sampling effect? *Oikos*, **95**, 161-170.

Weigelt A., Weisser W. W., Buchmann N. & Scherer-Lorenzen M. (2009). Biodiversity for multifunctional grasslands: equal productivity in high-diversity low-input and low-diversity high-input systems. *Biogeosciences Discussions*, **6**, 3187-3214.

Summary

Biodiversity is declining world-wide due to land-use change, urbanization, global warming and other anthropogenic transformations of the environment. Accumulating empirical evidence suggests that this ongoing pauperization of ecosystems impairs ecosystem functioning and thereby threatens human well-being. For assessing the consequences of species extinctions as well as for a prioritization of conservation efforts, a thorough understanding of the relationships between biodiversity and ecosystem functioning is required. In the past, numerous experiments have shown that an increase in biodiversity usually enhances community productivity but we are only beginning to understand why. In this thesis, I used data from a large-scale grassland biodiversity experiment (Jena Experiment) to explore mechanisms underlying positive relationships between plant diversity and aboveground primary productivity.

In **chapter 1**, I used different methodological approaches to assess the contributions of multiple species vs. single species effects to enhanced biomass production in species-rich communities. The results that I obtained strongly suggested that positive biodiversity effects persisted over multiple years and that beneficial interactions between different species increased over time. I demonstrated a positive effect of legumes on community biomass but I was able to show that their presence was not the main driver of the positive biodiversity–productivity relationship observed in the Jena Experiment. The presence of tall herbs increased community biomass as well and even small herbs and grasses had a positive effect if present in particular proportions. I found evidence for facilitation among species belonging to different functional groups and I could show that transgressive overyielding occurred more regularly than previously assumed.

In **chapter 2**, I examined temporal trends in the performance of species growing in monocultures or mixtures. My aim was to assess whether monocultures and mixtures differ with regard to changes in their productivity and to gain a better understanding why net biodiversity effects tend to increase over time. I observed that mixtures did generally better than monocultures, possibly due to a release from specialist soil or foliar pathogens. However, I found no support for the hypothesis that increasing net effects were mainly the result of monocultures degrading over time. In contrast, the results suggested that species that improved their performance in mixtures due to beneficial interactions with other species caused the net biodiversity effect to increase during the second phase of our observation period.

Chapter 3 is the documentation of botanical data from the Jena Experiment. Information on the biomass and cover for the individual plant species as well as for the entire

communities is reported. Furthermore, this chapter contains leaf area index (LAI) and height data at the community level. Most variables were measured twice per year during 2002–2008. This data set represents one of the largest and most detailed of its kind. It may be used for assessing various questions in the context of biodiversity–ecosystem functioning research. It is particularly valuable for exploring how effects of species richness or functional group richness on ecosystem properties change over time.

In **chapter 4**, I assessed whether positive effects of biodiversity on community biomass production were predominantly caused by an increase in the mean size or the density of individual plants. I hypothesized that increasing species richness would lead to a decrease in the overlap of niches among individual plants. As a result, I expected changing size–density–yield relationships across the species richness gradient. My data supported this assumption and suggested that diversity-induced increases in productivity were mainly caused by diversity-induced changes in plant density. In contrast, diversity-independent increases in productivity were related to an increase in plant size. I concluded that the mechanisms leading to enhanced productivity of species-rich as compared with species-poor communities cannot be derived from mechanisms explaining high productivity within communities that contain a particular number of species.

Zusammenfassung

Weltweit geht die Biodiversität aufgrund von Landnutzungsänderungen, Verstädterung, globaler Klimaerwärmung und anderen vom Menschen verursachten Veränderungen der Umwelt zurück. Zunehmend deuten empirische Daten darauf hin, dass diese fortschreitende Verarmung von Ökosystemen deren Funktionsweise beeinträchtigt und somit das Wohlergehen der Menschheit gefährdet. Um die Konsequenzen des Artensterbens abzuschätzen und Prioritäten im Naturschutz zu treffen, ist ein genaues Verständnis der Zusammenhänge zwischen Biodiversität und Ökosystemenfunktionen erforderlich. Eine Vielzahl von Experimenten hat in der Vergangenheit gezeigt, dass eine Zunahme der Biodiversität üblicherweise mit einer Erhöhung der Produktivität einer Gemeinschaft einhergeht, jedoch beginnen wir die Ursachen hierfür erst langsam zu verstehen. In der vorliegenden Arbeit nutzte ich Daten aus einem großflächigen Grünland-Biodiversitäts-Experiment (Jena Experiment), um Mechanismen zu untersuchen, die positiven Beziehungen zwischen Pflanzen-Diversität und oberirdischer primärer Produktivität zugrunde liegen.

Im **ersten Kapitel** bestimmte ich mittels unterschiedlicher methodischer Ansätze wie sehr Effekte mehrerer Arten im Gegensatz zu Effekten einzelner Arten zur erhöhten Biomasseproduktion in artenreichen Gemeinschaften beitrugen. Die erzielten Ergebnisse deuteten stark darauf hin, dass positive Biodiversitätseffekte über mehrere Jahre hinweg bestehen blieben und dass vorteilhafte Interaktionen zwischen verschiedenen Arten mit der Zeit zunahmen. Ich wies einen positiven Effekt von Leguminosen auf die Biomasse der Pflanzengemeinschaft nach, war aber in der Lage zu zeigen, dass die Anwesenheit von Leguminosen nicht die hauptsächliche Ursache für die positive Biodiversitäts–Produktivitäts Beziehung im Jena Experiment war. Auch die Präsenz großer Kräuter erhöhte die Biomasse einer Pflanzengemeinschaft und sogar kleine Kräuter und Gräser hatten auf diese einen positiven Effekt, wenn sie mit einem bestimmten Prozentsatz an der Gesamtbiomasse Anteil hatten. Ich fand Hinweise auf direkte positive Interaktionen (facilitation) zwischen Arten verschiedener funktioneller Gruppen und zeigte, dass eine Steigerung des Ertrags einer Mischung über den Ertrag der produktivsten Vergleichs-Monokultur hinaus (transgressive overyielding) mit größerer Regelmäßigkeit auftrat als bisher angenommen.

Im **zweiten Kapitel** untersuchte ich zeitliche Trends in der Ertragsleistung von Arten, die entweder als Monokulturen oder in Mischungen wuchsen. Mein Ziel war es zu klären, ob es Unterschiede in der Veränderung der Produktivität zwischen Monokulturen und Mischungen gibt und ein besseres Verständnis darüber zu gewinnen, warum Netto-Biodiversitätseffekte häufig mit der Zeit ansteigen. Ich beobachtete, dass die Produktivität von Arten in Mischungen generell einen besseren zeitlichen Verlauf nahm als die der

Monokulturen. Dies könnte darauf zurückzuführen sein, dass eine Art in Mischung möglicherweise weniger von spezialisierten Boden- oder Blatt-Pathogenen befallen wird als in Monokultur. Jedoch stützten meine Analysen nicht die Hypothese, dass zeitlich ansteigende Netto-Biodiversitätseffekte hauptsächlich das Ergebnis von degradierenden Monokulturen waren. Im Gegenteil deuteten meine Ergebnisse darauf hin, dass Arten, die in Mischung ihre Ertragsleistung aufgrund von vorteilhaften Interaktionen mit anderen Arten erhöhten, für das Ansteigen des Netto-Biodiversitätseffekts während der zweiten Phase des Beobachtungszeitraums verantwortlich waren.

Das **dritte Kapitel** dieser Arbeit ist eine Dokumentation von botanischen Daten aus dem Jena Experiment. Es werden Informationen über Biomasse und Deckungsgrad sowohl für die verschiedenen Pflanzenarten als auch für die gesamten Pflanzengemeinschaften zur Verfügung gestellt. Darüber hinaus enhält dieses Kapitel Blattflächenindex (LAI)- und Höhendaten, die jeweils für dem Niveau der gesamten Pflanzengemeinschaft ermittelt wurden. Die meisten Variablen wurden zweimal jährlich im Zeitraum 2002–2008 gemessen. Dieser Datensatz stellt einen der größten und detailliertesten seiner Art dar. Er kann für das Bearbeiten von verschiedenen Fragestellungen im Kontext der Erforschung von Zusammenhängen zwischen Biodiversität und Ökosytemfunktionen genutzt werden. Er ist besonders nützlich um zu erkunden, wie sich Effekte der Artenzahl oder der Anzahl der funktionellen Gruppen auf Ökosystemeigenschaften mit der Zeit verändern.

Im **vierten Kapitel** analysierte ich, ob positive Biodiversitätseffekte auf die Biomasse einer Pflanzengemeinschaft hauptsächlich durch die Zunahme der mittleren Größe oder der Dichte der einzelnen Pflanzen hervorgerufen werden. Ich stellte die Hypothese auf, dass sich die Nischen der einzelnen Pflanzen mit zunehmender Artenzahl immer weniger überschneiden. Als Folge erwartete ich, dass sich das Verhältnis von Größe, Dichte und Ertrag entlang des Artenzahl-Gradienten ändern würde. Meine Daten unterstützen diese Vermutung und deuteten darauf hin, dass diversitätsinduzierte Produktivitätssteigerungen hauptsächlich durch diversitätsinduzierte Veränderungen in der Pflanzendichte hervorgerufen wurden. Im Gegensatz dazu standen diversitätsunabhängige Produktivitätssteigerungen im Zusammenhang mit einer Zunahme der Pflanzengröße. Ich schlussfolgerte, dass die Mechanismen, die zu einer erhöhten Produktivität von artenreichen Pflanzengemeinschaften führen, nicht von Mechanismen abgeleitet werden können, die eine hohe Produktivität innerhalb von Pflanzengemeinschaften erklären, die eine bestimmte Anzahl von Arten enthalten.

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Publications

Peer-reviewed

Marquard E., Weigelt A., Roscher C., Gubsch M., Lipowsky A., Schmid B. (2009): "Positive biodiversity–productivity relationship due to increased plant density", *Journal of Ecology*, doi: 10.1111/j.1365-2745.2009.01521.x.

Marquard E., Weigelt A., Temperton V., Roscher C., Schumacher J., Buchmann N., Fischer M., Weisser W., Schmid B. (2009): "Plant species richness and functional composition drive overyielding in a 6-year grassland experiment", *Ecology*, in press.

Hooftman D., Oostermeijer G., **Marquard E.**, den Nijs H. (2008): "Modelling the consequences of crop-wild relative gene flow: a sensitivity analysis of the effects of outcrossing rates and hybrid vigour breakdown in Lactuca", *Journal of Applied Ecology* 45(4):1094-1103.

Poux C., Madsen O., **Marquard E.**, Vieites D., de Jong W., Vences M. (2005): "Asynchronous colonization of Madagascar by the four endemic clades of primates, tenrecs, carnivores, and rodents as inferred from nuclear genes", *Systematic Biology* 54(5): 719-730.

Other publications

Fischer M., Rottstock T., **Marquard E.**, Middelhoff C., Roscher C., Temperton V., Oelmann Y., Weigelt A. (2008): "L'expérience de Iéna démontre les avantages de la diversité végétale pour les prairies", *Fourrages* 195: 275-286.

Marquard E., Durka W. (2005): "Auswirkungen des Anbaus gentechnisch veränderter Pflanzen auf Umwelt und Gesundheit: Potentielle Schäden und Monitoring"; Bericht für das Sächsische Ministerium für Umwelt und Landwirtschaft. http://www.umwelt.sachsen.de/umwelt/download/gentechnik/Auswirkungen_des_Anbaus.pdf